

CHAPTER EIGHT

Niche dimensionality and ecological speciation

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The ecological niche plays a central role in the process of ‘ecological speciation’, in which divergent selection between niches drives the evolution of reproductive isolation (Muller 1942; Mayr 1947, 1963; Schlüter & Nagel 1995; Funk 1998; Schlüter 2000). Ecological by-product speciation occurs because ecological traits that have diverged between populations via divergent selection, or traits that are genetically correlated with such traits, incidentally affect reproductive isolation. This process can occur under any geographic arrangement of populations (e.g. allopatry, parapatry or sympatry). A central prediction of this process is that ecologically divergent pairs of populations will exhibit greater levels of reproductive isolation than ecologically similar pairs of populations of similar age. Another prediction is that traits under divergent selection, or those genetically correlated with them, should often incidentally affect reproductive isolation (e.g. mate preference, hybrid fitness). In recent years, these predictions have been supported in a range of taxa (see Feder *et al.* 1994; Funk 1998; Via 1999; Rundle *et al.* 2000; Jiggins *et al.* 2001; Funk *et al.* 2002, 2006; Bradshaw & Schemske 2003; Rundle & Nosil 2005; and Funk, this volume, for review), and processes such as resource competition and predation are now known to be involved (Mallet & Barton 1989; Schlüter 1994; Rundle *et al.* 2003; Vamosi 2005; Nosil & Crespi 2006a).

However, ecological divergence often results in patterns inconsistent with the completion of speciation, such as imperfect reproductive isolation and weak genotypic clustering (Drès & Mallet 2002; Coyne & Orr 2004; Nosil *et al.* 2005; Rundle & Nosil 2005; Nosil 2007). Moreover, the collapse of distinct species pairs formed by selection has been documented (Hubbs 1955; Arnold 1997; Seehausen *et al.* 1997; Taylor *et al.* 2006; Richmond & Jockusch 2007). What factors determine the likelihood that divergent selection completes speciation, and that distinct species are maintained? In the broadest sense, divergence during speciation is often continuous in nature (even if the end point of this continuous process is the development of a discontinuity). For example, the magnitude of reproductive isolation can vary quantitatively (Coyne & Orr 2004), as can the degree of genotypic clustering (Jiggins & Mallet 2001), and the extent

of monophyly in gene genealogies (Dopman *et al.* 2005). These different degrees of divergence can be thought of as arbitrary ‘stages’ of the continuous process of speciation (Drès & Mallet 2002; de Queiroz 2005; Mallet *et al.* 2007; Hey, this volume), with greater divergence equating to greater progress towards the completion of speciation. What factors predict this degree of progress?

Three relatively well-considered factors for variability in progress towards speciation are genetic architecture, time since divergence, and levels of gene flow. For example, speciation is promoted by pleiotropic effects on reproductive isolation of genes under selection (Rice & Salt 1990; Rice & Hostert 1993; Boughman 2002; Kirkpatrick & Ravigné 2002; Bradshaw & Schemske 2003), physical linkage of genes under selection and those conferring reproductive isolation (Hawthorne & Via 2001; Noor *et al.* 2001; Rieseberg 2001), one-allele assortative mating mechanisms (Felsenstein 1981; Ortíz-Barrientos & Noor 2005; Rundle & Nosil 2005 for review), increased time since divergence (Coyne & Orr 2004) and geographic barriers to gene flow (Gavrilets 2004; Bridle and Vines, this volume).

An alternative, and less-considered, explanation for the degree of progress towards ecological speciation concerns the number of niche dimensions in which pairs of taxa differ. One aspect of the niche, that dealing with the environmental requirements of species (Chase & Leibold 2003), can be related to fitness landscapes, with species’ niches corresponding to peaks on that landscape (Simpson 1944; Schlüter 2000). This landscape can vary in any number of ecological dimensions, with divergence in a greater number of dimensions potentially promoting speciation. This ‘niche dimensionality hypothesis’ is the focus of this chapter, and the alternative causal interpretation, that speciation facilitates increased dimensionality of niche divergence, is addressed in a latter section of the chapter. We also note that geographic, genetic, time-based and ecological hypotheses for the degree of progress towards speciation are not mutually exclusive.

Dimensionality in niche divergence and speciation

the stronger [a population’s] need for local adaptation ... the greater the probability of changes in the components of isolating mechanisms

Mayr (1963)

The magnitude, targets and causes of divergent selection are affected by ecological conditions (Endler 1977; Reimchen 1979; Endler 1986; Schlüter 2000; Kingsolver *et al.* 2001; Grant & Grant 2002). Thus, in addition to genetic scenarios, there are also specific ecological scenarios that might facilitate speciation. As exemplified by Mayr’s quote, it is generally believed that as populations become more locally adapted, the probability of speciation increases. However, what is meant by ‘stronger’ local adaptation?

One answer is adaptation to a great number of ecological axes (i.e. dimensions). The nature of the ecological niche has received continued study over the

last century (Grinnell 1917; Elton 1927; Hutchinson 1957, 1959; Pianka 1978; Schoener 1989; Wiens & Graham 2005). A major aspect of the ecological niche is its dimensionality (Hutchinson 1957; Harmon *et al.* 2005). According to this concept, an organism's niche is defined by numerous biotic and abiotic variables, each of which can be considered an axis in multidimensional space. The dimensionality of the ecological niche can be assessed using measurements of ecological variables (Maguire 1967; Green 1971) or phenotypic variables that interact with the environment to determine fitness (Vandermeer 1972; Harmon *et al.* 2005). For example, in a given species, selection might act on morphology ('dimension 1' – e.g. seed size), physiology ('dimension 2' – e.g. optimal temperature) or both.

Divergent selection between niches is a central component of ecological speciation, but little is known about whether niche dimensionality affects speciation. A distinction between considering niche dimensionality for a species versus for the process of speciation is that *differences in the niche among pairs (or sets) of taxa* must be examined for the latter (rather than niche properties of a single taxon). Here, the focus is on dimensionality of niche divergence, rather than niche dimensionality. This point is critical. For example, sets of populations that each individually exhibit highly dimensional niches would not exhibit highly dimensional niche divergence if their niches were similar to one another in all axes. In essence, as niches differ in more dimensions, they become more 'discrete', thereby promoting phenotypic divergence. The number of niche dimensions that pairs of taxa differ in can be measured and related to speciation using the following three steps (illustrated in Fig. 8.1).

First, axes of niche differentiation (e.g. trait differentiation as a surrogate) must be measured for all taxa. This could be achieved using measurements of ecological variables (Maguire 1967; Green 1971), phenotypic traits that determine fitness (Vandermeer 1972; Harmon *et al.* 2005) or direct measurements of natural selection (Lande & Arnold 2001; Schlüter 2000; Kingsolver *et al.* 2001). The focus here is on ecological traits that mediate interactions between organisms and aspects of their biotic or abiotic environment. Figure 8.1 depicts how pairs of taxa can potentially be subject to divergent selection on two different abiotic ecological axes, and can differ in mean phenotype in these two axes.

Second, the dimensionality of niche divergence is quantified. Exactly what is considered a 'dimension' or an 'axis' can vary, but a critical point is that different dimensions should be independent. Ideally, ecologically relevant and statistically independent axes can be identified (Green 1971; Harmon *et al.* 2005), but genetic and functional independence could also be considered. For example, sets of functionally related traits might be pooled to make more general dimensions (e.g. all morphological traits related to foraging used to construct a 'foraging morphology' dimension). When it comes to quantifying the dimensionality

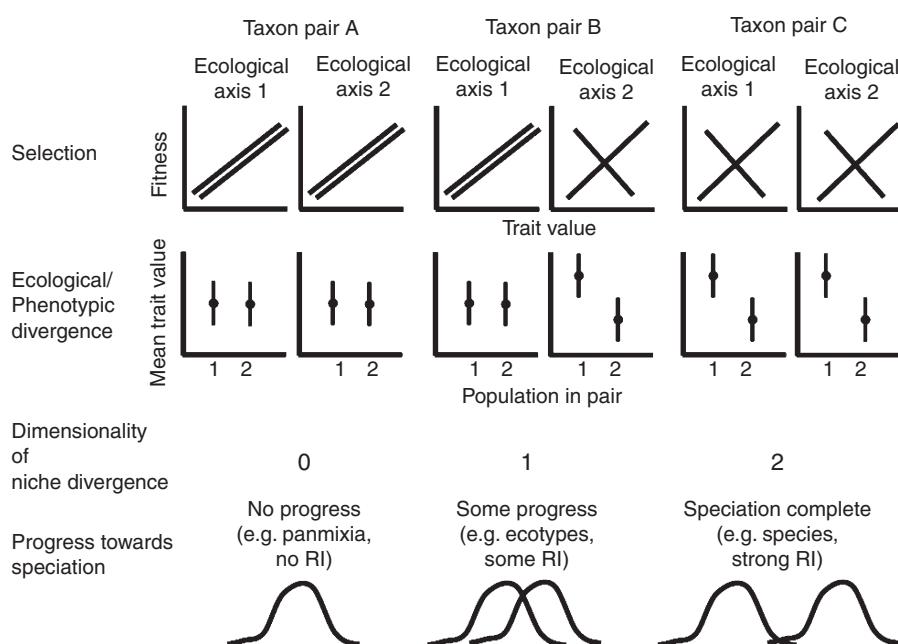


Figure 8.1 Schematic diagram of variation among pairs of taxa in the number of dimensions (i.e. ecological axes) their niches vary in, and the potential effects on speciation. There are two ecological axes (e.g. measured by the phenotypic surrogates morphology and physiology). Taxon pair A does not differ along either niche axis, and shows no progress towards speciation. Taxon pair B differs along a single niche axis, and exhibits partial progress towards speciation. Taxon pair C differs along both niche axes, and exhibits the greatest progress towards speciation.

of niche divergence, if niche dimensions do not appear highly correlated then one approach is to simply count up the number of niche dimensions that pairs of taxa differ in. Figure 8.1 depicts how pairs of taxa can differ in zero, one or two dimensions. More quantitative descriptions of the degree to which taxa differ along different axes could also be constructed. For example, one could calculate an among-taxa variance – covariance matrix of various niche axes. There are then various statistical techniques that could be used to measure the effective dimensionality of this matrix (Schluter 2000; Herrera *et al.* 2002; Blows & Hoffman 2005; McGuigan *et al.* 2005; Mezey & Houle 2005; Chenoweth & Blows 2006; Hine & Blows 2006; Van Homrigh *et al.* 2007). In general, multivariate statistics can be used to generate independent niche dimensions (as in the example with *Timema* walking-stick insects below).

In considering statistical independence of ‘dimensions’, it is important to realize that independence of different environmental variables which potentially cause niche divergence may or may not come with independence of the

axes of corresponding trait divergence (see Seehausen, this volume). Take the example of fish in a lake: water depth and distance from shore are statistically non-independent, yet they may select divergently on genetically independent traits (e.g. visual system and predator avoidance behaviour, respectively). Conversely, water depth and water turbidity are statistically independent. Yet, they may reinforce each other in selecting divergently on the same trait (e.g. colour vision). Ultimately, it is probably the number of genetically independent axes of trait divergence that determines the progress to ecological speciation.

Third, dimensionality of niche divergence is related to measures of progress towards speciation. Examples of such measures are experimental estimates of reproductive isolation, the degree of gene flow or genotypic clustering inferred from molecular markers and traditional taxonomic status. Higher levels of reproductive isolation, lower gene flow, increased genotypic clustering and higher taxonomic status (e.g. species versus ecotype) all indicate greater progress towards speciation (Mallet 1995; Schlüter 2000; Jiggins & Mallet 2001; Coyne & Orr 2004). This is best done with divergent conspecific populations, or recently formed species, to avoid conflating differences evolving after speciation with those involved in speciation. In a formal analysis, time since the initiation of divergent selection can be taken as a covariate.

Increased total selection strength

We emphasize that a general factor of interest here is the total strength of divergent selection that a population pair is exposed to, which could increase via selection on a greater number of ecological dimensions or simply via stronger selection on a single dimension. We argue that the former mechanism, divergent selection on more dimensions, may be important for generating increased total strength of selection in natural populations. For example, the degree of divergence along any single dimension is limited by the distance between adaptive peaks in that single dimension (Schlüter 2000), and may be further limited by lack of suitable genetic variation in that particular dimension (Futuyma *et al.* 1995) and by physical or functional constraints (Arnold 1992). Notably, if the total strength of selection goes up with greater dimensionality of niche divergence, the per locus selection coefficient does not necessarily decrease as more loci become involved in divergence. Finally, divergence involving more ecological niche dimensions likely also increases the number of genes involved. Because of this, if speciation requires epistasis (Dobzhansky-Muller incompatibilities, Bateson 1909; Dobzhansky 1936, 1937; Muller 1940, 1942; Orr 1995) or divergence in just a few key genes that affect reproductive isolation, then divergence in many dimensions (genes) may be more effective at promoting speciation than greater divergence in just one or a few dimensions (genes).

Substantial phenotypic divergence and speciation may commonly require multidimensional niche divergence.

Empirical evidence that dimensionality in niche divergence affects speciation

Laboratory experimental evolution studies

Laboratory experiments collectively indicate that multifarious ... divergent selection can readily lead to complete reproductive isolation, but that single-factor ... divergent selection will typically lead to only incomplete reproductive isolation

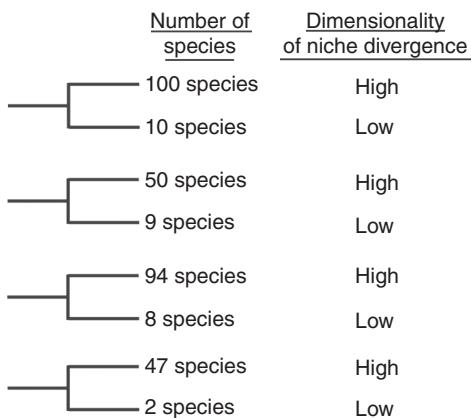
Rice and Hostert (1993, pp. 1647)

Laboratory selection experiments provide ideal opportunities for testing how dimensionality in niche divergence affects speciation. Replicate lines could be selected divergently on zero, one, two or more traits (i.e. dimensions), controlling for the total strength of selection. At the end of the experiment, one can test whether lines selected divergently for more traits exhibit greater reproductive isolation (Fig. 8.2). Rice and Hostert (1993) reviewed 38 selection experiments aimed at producing speciation in the lab, and concluded that selection on more traits promotes speciation.

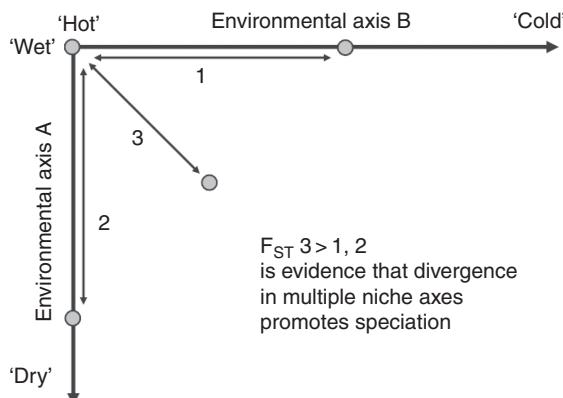
To assess the status of this conclusion fourteen years later, using a new and relevant classification scheme, a literature review was conducted using 59 studies recovered from Rice and Hostert (1993) and a Web of Science search on the terms ‘selection and experiment and speciation’. The studies were subdivided into whether they imposed selection directly on premating isolation or on a non-isolation trait (e.g. sternopleural bristle number), and according to whether selection was imposed with or without gene flow (following Kirkpatrick & Ravigné 2002). Table 8.1 provides details concerning this scheme.

The most obvious point emerging from the survey is that experiments allowing strong comparisons are lacking. No single study has selected on one versus multiple traits. Only five studies applied selection on more than one trait, but there was some suggestion that these five were more successful at evolving reproductive isolation than those selecting on a single trait. For experiments involving direct selection, all three experiments that selected on more than one trait resulted in the evolution of near complete premating isolation. In contrast, only one of 13 experiments that imposed direct selection on only a single trait resulted in near complete premating isolation. However, comparison within gene-flow categories is not possible, because all studies selecting directly on multiple traits also involved gene flow. For indirect selection, one of two experiments selecting on multiple traits evolved consistent, but partial, premating isolation. In contrast, only 11 of 42 experiments selecting on a single trait resulted in consistent, but partial,

(a) Phylogenetic test



(b) Population genetic test



(c) Experimental evolution test

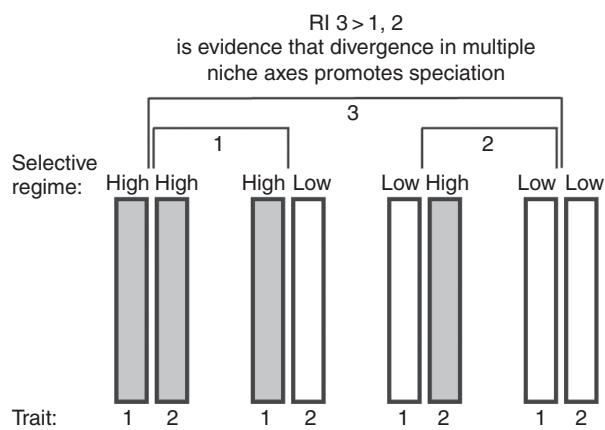


Figure 8.2 Tests for whether the number of niche dimensions that pairs of taxa differ in affects progress towards speciation. See text for details. (a) Phylogenetic test. (b) Population genetic test. (c) Experimental evolution test.

Table 8.1 Summary of 59 laboratory speciation experiments in relation to the type of selection imposed, and number of traits subject to selection.

	No. of studies	Result	No. of traits	References
(1) No Gene Flow Direct	7	Mixed RI	1	1–7
	5	Partial RI	1	8–12
	1	Strong RI	1	13
(2) No Gene Flow Indirect	7	No RI	1	14–20
	2	Mixed RI	1	17, 21
	8	Partial RI	1	22–28
	1	No RI	4	29
	1	Partial RI	2	30
(3) Gene Flow Direct	3	Strong RI	4	31–33
(4) Gene Flow Indirect	21	No RI	1	10, 24, 34–38
	1	Mixed RI	1	39
	3	Partial RI	1	25, 27, 40

Note: No RI refers to a lack of significant RI in all cases. Mixed RI refers to cases where partial RI was detected in some cases, but RI varied among year, replicates and strains such that RI was sometimes lacking. Partial RI refers to consistent patterns of incomplete RI. Strong RI refers to over 90 percent assortative mating. (1) No Gene Flow Direct. These experiments destroy-all-hybrids and impose selection directly on reproductive isolation during the course of the experiment. (2) No Gene Flow Indirect. These experiments impose selection on a non-isolation trait(s) during the experiment, and then testing for premating isolation at the end of the experiment. (3) Gene Flow Direct Experiments. These impose selection on reproductive isolation during the course of the experiment, but not all hybrids are destroyed. (4) Gene Flow Indirect Experiments. These impose selection on a non-isolation trait(s) during the course of the experiment, not all hybrids are destroyed, and RI is measured at the end of the experiment.

1 = Barker & Karlsson 1974; 2 = Ehrman 1971; 3 = Ehrman 1973; 4 = Ehrman 1979; 5 = Kessler 1966; 6 = Koepfer 1987; 7 = Wallace 1953; 8 = Crossley 1974; 9 = Dobzhansky *et al.* 1976; 10 = Hostert 1997; 11 = Knight *et al.* 1956; 12 = Koopman 1950; 13 = Paterniani 1969; 14 = Barker & Cummins 1969; 15 = Ehrman 1964; 16 = Ehrman 1969; 17 = Markow 1981; 18 = Mooers *et al.* 1999; 19 = Santibanez & Waddington 1958; 20 = van Dijken & Scharloo 1979; 21 = Halliburton & Gall 1981; 22 = de Oliveira & Cordeiro 1980; 23 = del Solar 1966; 24 = Dodd 1989; 25 = Grant & Mettler 1969; 26 = Hurd & Eisenburg 1975; 27 = Rundle *et al.* 2005; 28 = Soans *et al.* 1974; 29 = Rundle 2003; 30 = Killias *et al.* 1980; 31 = Rice 1985; 32 = Rice & Salt 1988; 33 = Rice & Salt 1990; 34 = Chabora 1968; 35 = Scharloo 1971; 36 = Scharloo *et al.* 1967; 37 = Spiess & Wilke 1984; 38 = Thoday & Gibson 1970; 39 = Coyne & Grant 1972; 40 = Thoday & Gibson 1962.

premating isolation. Factors not considered here, such as variation in effective population size (Ödeen & Florin 2000; Florin & Ödeen 2002) or a ‘file-drawer effect’ from unpublished results, could affect the patterns reported here. Thus although trends are consistent with the idea that selection on

more traits promotes speciation, experimental evolution studies explicitly designed to test this hypothesis would be useful.

Data from natural populations of *Timema* walking-stick insects

Dimensionality in divergence of cryptic colour patterns

Timema are wingless insects inhabiting the chaparral of southwestern North America (Vickery 1993; Crespi & Sandoval 2000). Individuals feed and mate exclusively on the host plants upon which they live, and many species exhibit host-plant ecotypes (defined by the host they are found upon). A major axis of host-related differentiation in these insects is cryptic colouration (Sandoval 1994a,b; Crespi & Sandoval 2000; Nosil & Crespi 2006a). The phenotypic dimensionality of divergence in cryptic colouration between populations of *Timema* that had not completely speciated (conspecific host ecotypes using different plants) was compared to that between species ($n=14$ ecotypes from eight species, where species are designated based upon taxonomic classification). The traits examined are the six colour measurements reported in Nosil and Crespi (2006a; hue, saturation and brightness of the exterior and central parts of the dorsal surface, which are all measured on similar scales, $n=1032$ individuals). Each of these traits was comprised of three measurements for the exterior body parts (one measurement on each of head, abdomen and thorax) and two measurements for the central body parts (one measurement on each of abdomen and thorax). Using these 15 raw measurements, all pairwise differences in colour measurements between different species and between distinct ecotypes within species were calculated (Kirkpatrick & Lofsvold 1992). These differences were then averaged to yield the six traits examined in Nosil and Crespi (2006a; e.g. differences between the hue measurements from the head, abdomen and thorax were average to calculate ‘mean difference in body hue’). The dimensionality of each set of comparisons was then calculated based on the variance-covariance matrix of differences among the colour axes. Since the direction of subtraction for each pair was arbitrary, all variances were calculated with a mean of zero and covariances were forced through the origin.

The concept is visualized in Fig. 8.3, which shows the amount of the variance explained by each of m independent directions, for ecotypes versus species pairs. Each direction is a composite trait, made up from a linear combination of the original traits. The dimensionality (‘evenness’) of each matrix was calculated from its eigenvalues using Levene’s index (see Schlüter 2000, pp. 220–221, for details)

$$L = \frac{1}{\sum p_i^2}$$

where p_i is the proportion of total variance accounted for by the direction i . $L=1$ if all variance is in the first direction, and $L=m$, the number of traits, if variance

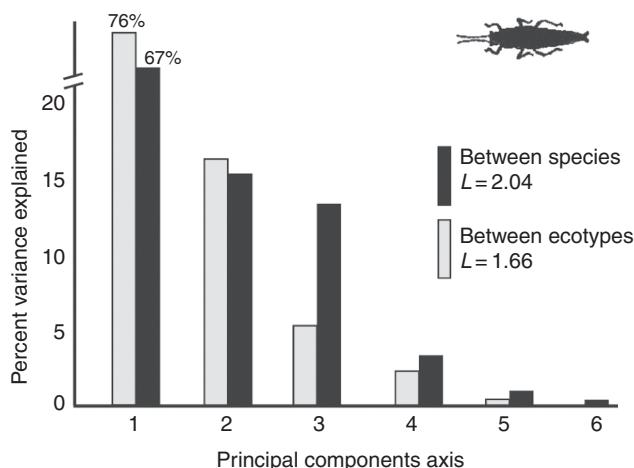


Figure 8.3 Phenotypic dimensionality of colour-pattern divergence is greater between *Timema* species versus between ecotypes within species. Dimensionality was calculated based on the variance-covariance matrix of differences among the colour axes, using the Levene's index (L) (larger values indicate more 'evenness', and thus greater dimensionality).

is equitably distributed. L is therefore a useful measure of 'phenotypic dimensionality'. Dimensionality was lower for comparisons between ecotypes ($L = 1.66$) versus between distinct species ($L = 2.04$), with marked differences in the distribution of eigenvalues (Fig. 8.3). It is hard to infer causality from these data, which also suffer from lack of replication, but certainly they suggest that distinct species exhibit greater dimensionality in cryptic colouration than do ecotypes which did not fully speciate.

Dimensionality in divergence in morphology and physiology

Another avenue is to examine divergence in two different axes of host-related differentiation: cryptic morphology and physiological adaptation to different hosts. Consider two species, *Timema podura* and *Timema cristinae*, who are not sister-species and whose geographic ranges do not overlap (Law & Crespi 2002; Sandoval & Nosil 2005). Both species are composed of two host-plant ecotypes (the '*Ceanothus* ecotype' and the '*Adenostoma* ecotype'), and divergent host-adaptation has driven the evolution of various forms of reproductive isolation between ecotypes in both species (Nosil *et al.* 2002, 2003, 2005, 2006a,b; Nosil 2004; Sandoval & Nosil 2005; Nosil & Crespi 2006b). However, speciation (e.g. reproductive isolation) between ecotypes is incomplete in both species (see Nosil 2007 for details). The main argument for incomplete speciation focuses on the observation that divergence tends to be weaker in parapatry than in allopatry, a classic signature of gene flow, and thus incomplete reproductive isolation, between parapatric populations (Coyne & Orr 2004). In *T. cristinae*, this pattern of weaker divergence in parapatry is observed for experimental estimates of reproductive isolation (Nosil 2007), for mitochondrial and nuclear genetic differentiation (Nosil *et al.* 2003, unpublished), and for morphological traits relevant to host-plant adaptation

(Sandoval 1994a; Nosil & Crespi 2004). Moreover, bimodality in morphological traits is weak and often collapses in parapatry, indicative of incomplete reproductive isolation (Mallet 1995; Jiggins & Mallet 2001). Finally, there is no evidence for F1 hybrid egg inviability in ‘hybrids’ between the ecotypes (Nosil *et al.* 2007). Similar trends are observed in *T. podura*, although data are scarcer (Vickery 1993; Law & Crespi 2002; Sandoval & Nosil 2005; Nosil unpublished).

In ecotypes of both species, there is evidence for strong divergent selection, but only along the single axis of cryptic morphology. For example, controlled predation trials with jays reveal strong fitness trade-offs between hosts for ecotypes of both species (Sandoval 1994b; Sandoval & Nosil 2005). In *T. cristinae*, a manipulative field experiment revealed strong, host-specific divergent selection on morphology in the presence, but not in the absence, of visual predation (Nosil & Crespi 2006a). Thus, there is no evidence for divergent selection acting on morphology independent of crypsis (e.g. biomechanical/manoeuvring reasons). When physiology is considered, again divergent selection is lacking. In field reciprocal-transplant experiments conducted in the absence of predation, both ecotypes of both species show higher fecundity when reared on *Ceanothus* (Sandoval & Nosil 2005). Perhaps the unidimensionality of divergent selection explains why only partial progress towards speciation has occurred.

Data allowing strong inferences are unavailable, but preliminary data among other species of *Timema* provide some insight. Divergence in host-plant use varies extremely within the genus *Timema*. For example, pairs of populations can use hosts in the same plant genus, hosts in different plant genera that are in the same plant division (e.g. two angiosperm species), or different plant divisions (i.e. one angiosperm host and one gymnosperm host). The latter category is an extreme form of divergence in host-plant use, not only within *Timema*, but among herbivorous insects in general (Ehrlich & Raven 1964; Bernays & Chapman 1994; Crespi & Sandoval 2000; Nosil 2002; Winkler & Mitter 2007). Preliminary host preference data from 68 populations spanning eight *Timema* species show a substantial increase in habitat isolation between taxon pairs with increasing taxonomic divergence in host-plant use (Nosil unpublished). This suggests that extreme host-shifts (i.e. between taxonomically divergent plant species) are required for very strong reproductive isolation to evolve. Perhaps highly dimensional divergent selection occurs only when divergence in host use is extreme. For example, physiological trade-offs are most likely when there are shifts between taxonomically divergent hosts (which are also chemically divergent; Winkler & Mitter 2007). This model of *Timema* speciation is depicted in Fig. 8.4.

Other empirical tests

A number of other tests for an association between dimensionality in niche divergence and speciation are possible. A phylogenetic test would use methods

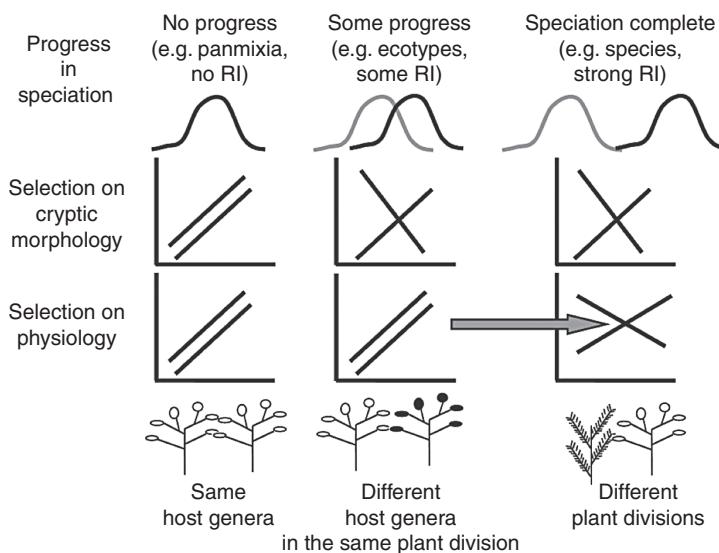


Figure 8.4 A model of speciation in *Timema* stick-insects, where speciation is promoted by more extreme host-plant shifts, which increase the dimensionality of niche divergence. The graphs depict fitness (y-axis) against trait value (x-axis) for cryptic morphology and physiology. The critical shift in selective regime that predicts transitions across the species boundary is labelled with a grey arrow. Population pairs using the same host (left) are not exposed to divergent selection. Pairs using moderately different hosts (center) are exposed to divergent selection only along a single axis (crypsis). Pairs using extremely different hosts (right) are exposed to divergent selection along both axes.

for identifying variability in net diversification (speciation minus extinction) rates (Mitter *et al.* 1988; Slowinski & Guyer 1989; Hey 1992; Nee *et al.* 1992; Harvey *et al.* 1994; Chan & Moore 2002; Ree 2005; Vamosi & Vamosi 2005). The general idea would be to quantify the dimensionality of differences between taxa within clades (Arnqvist 1998; Warheit *et al.* 1999; Cornwell *et al.* 2006), and then test if this is related to variation in diversification rate among clades. For example, a consistent, positive association across sister-clades between the dimensionality of differences between taxa and species richness could mean that dimensionality in niche divergence is associated with net diversification rate (Fig. 8.2a).

A population genetic test would examine the relationship between ecological divergence and neutral genetic differentiation. Specifically, when ecological divergence causes the evolution of reproductive barriers, it can result in a general barrier to even neutral gene flow (Barton & Bengtsson 1986; Charlesworth *et al.* 1997; Pialek & Barton 1997; Gavrilets & Cruzan 1998; see Gavrilets 2004, pp. 147–148, for summary). General barriers reduce the homogenizing effects of gene flow across the genome, thereby allowing these neutral

regions to diverge via genetic drift. If neutral gene flow decreases as adaptive divergence increases, the resulting increase in drift may result in a positive correlation between the degree of adaptive phenotypic divergence and differentiation at neutral loci (independent from the geographic distance between populations). Several studies have reported this pattern (MacCallum *et al.* 1998; Lu & Bernatchez 1999; Cooper 2000; Ogden & Thorpe 2002; Vines *et al.* 2003; Rocha *et al.* 2005; Grahame *et al.* 2006; Parchman *et al.* 2006; Pilot *et al.* 2006), and their basic design could be modified to examine the role of dimensionality in niche divergence (Fig. 8.2b). The modification requires gradients in two or more ecological variables. Population pairs could be sampled along a single (e.g. dry-hot) or multiple gradients (e.g. dry-hot and wet-cold). The prediction is that genetic differentiation would be greater, and thus gene flow lower, in the latter case.

Niche dimensionality and speciation: alternative mechanisms generating the association

To the extent that increased dimensionality in niche divergence results in greater genetic divergence, it must often promote speciation. This assumption of increased genetic divergence seems reasonable given that increased dimensionality in niche divergence might (1) subject a greater number of traits/genes to divergent selection, thereby increasing adaptive genetic divergence between populations, and (2) result in general barriers to gene flow to facilitate even neutral genetic divergence via genetic drift. However, a number of different mechanisms might generate association between dimensionality in niche divergence, genetic divergence and progress towards speciation. These mechanisms can be viewed as alternative hypotheses concerning why niche dimensionality might affect speciation.

Increased genetic dimensions and ecologically dependent hybrid fitness

The genotype of a species is an integrated system adapted to the ecological niche in which the species lives. Gene recombination in ... hybrids may lead to ... discordant gene patterns
Dobzhansky (1951)

Ecological speciation often involves ecologically based reductions in hybrid fitness (Schluter 2000; Rundle & Whitlock 2001; Rundle & Nosil 2005). Hybrids exhibit low fitness because their intermediate phenotypes place them in valleys of low fitness in the fitness landscape. When adaptation to an additional ecological dimension involves divergence in an additional set of loci, hybrid fitness is expected to decrease with the number of dimensions. This can be conceptualized by considering recombinant hybrid genotypes: these genotypes can be ‘mismatched’ to the environment in one, two, three, etc. dimensions,

depending on how many sets of loci are each adapted to different ecological dimensions. Each set of independent loci can be thought of as a ‘genetic dimension’, with more dimensions resulting in lower fitness (Fig. 8.5a). This mechanism requires genetic dimensions that contribute independently to fitness; the extent to which this occurs is an open empirical question.

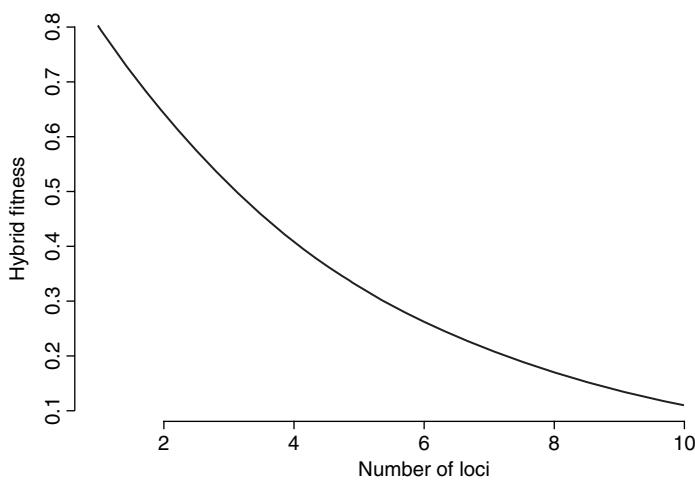
Changing fitness landscapes

A mechanism by which the dimensionality of fitness landscapes reduces hybrid fitness without increased genetic dimensionality involves changes in the shape of the landscape. Consider the circumstance in which each new axis has two distinct optimal phenotypic values. As the number of dimensions that peaks in the landscape differ in rises (Fig. 8.5b versus Fig. 8.5c), the overall distance between peaks increases, as does the depth of the fitness valley that hybrid phenotypes tend to fall within (Fig. 8.5d). Thus using simulations it can be shown that hybrid fitness, relative to parents, decreases as landscape dimensionality increases (Fig. 8.5e; see figure legend 8.5 for details). Notably, the same pattern would occur if peaks were simply moved further apart along any single dimension. Thus this mechanism is most likely to be important when the distance between peaks in any single dimension is limited (i.e. divergent selection along a single axis is weak), or when divergence between distant peaks is limited by lack of suitable genetic variation.

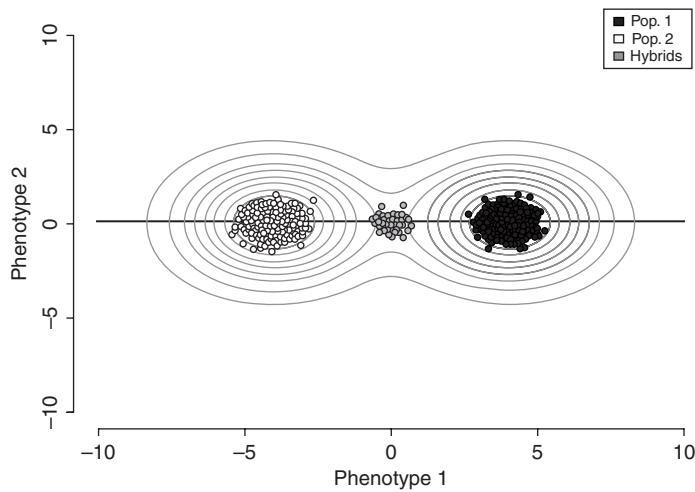
Pleiotropy

In the scenario directly above, the dimensionality of the fitness landscape itself changes. However, reductions in hybrid fitness can also occur without such changes due to the effects of pleiotropy on genetic variance (Turelli 1985; Wagner 1989). Consider a fitness landscape which has two separate optima that always differ in only a single dimension. Two distinct populations, each adapted to one of these two optima, were created using simulations (Guillaume & Rougemont 2006; see legend of Fig. 8.5 for details). In these simulations, traits were purely additive, and mutations had pleiotropic effects on all traits. Hybrids were formed by randomly selecting one parent from each population, and the average fitness of both hybrids and parents was calculated. The relative fitness distribution of the hybrids has a lower mean and variance when mutation affects two traits compared to when mutations affect a single trait (Fig. 8.5f). This occurs despite the fact that the distance between the peaks and their relative width is identical. Extending this result to more traits shows that mean hybrid fitness is negatively related to the number of traits pleiotropically affected by mutation (Fig. 8.5f). This effect can be attributed to a reduction in genetic variation along each axis in the parent population due to the pleiotropic effects of mutations (Turelli 1985; Wagner 1989). As the number of traits increases, hybrids become more concentrated in the ‘saddle’ of the selective

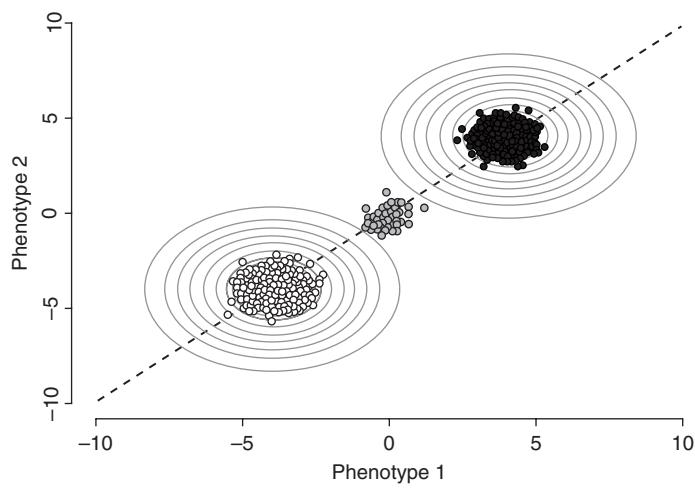
(a) Hybrid fitness with increasing genetic dimensions



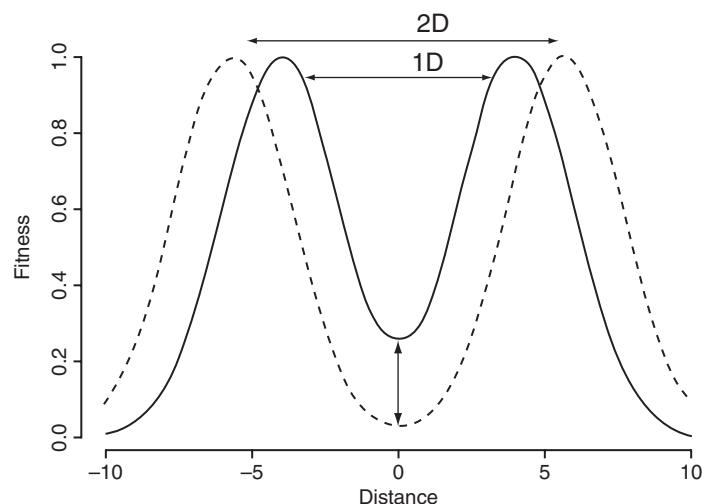
(b) Landscape differs in one dimension



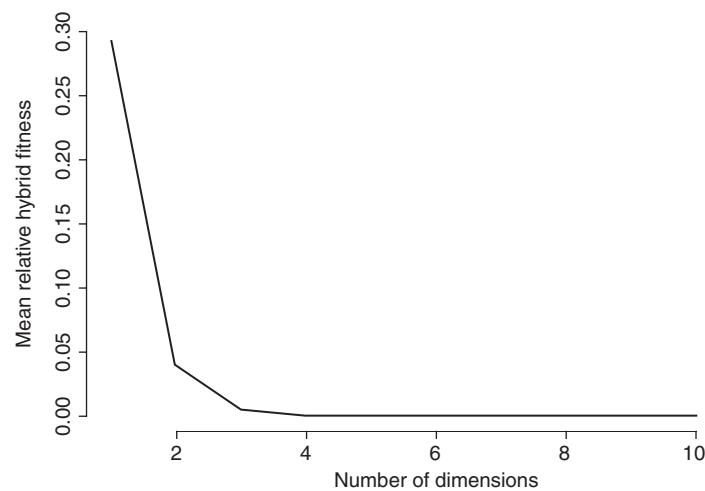
(c) Landscape differs in two dimensions

**Figure 8.5**

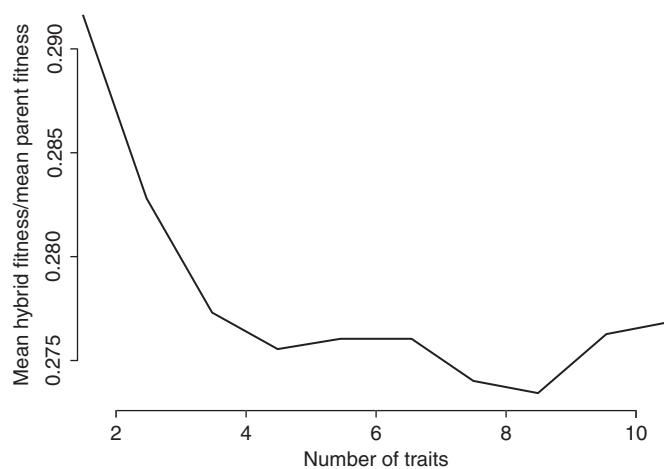
(d) Distance between peaks, 1D versus 2D



(e) Hybrid fitness as a function of dimensions



(f) Mean hybrid fitness in relation to number of traits



valley. The realism of this scenario might be questioned (as for models invoking pleiotropy in general, see below). However, less extreme scenarios should produce the same effect (i.e. mutations need not affect all traits), and it illustrates how hybrid fitness can be reduced without changing the fitness landscape itself.

Dobzhansky–Muller incompatibility models

A general class of speciation models involves the evolution of genetic incompatibilities in hybrids due to negative epistasis between alleles at different loci ('Dobzhansky–Muller incompatibilities'; Bateson 1909; Dobzhansky 1936, 1937; Muller 1940, 1942; Orr 1995; Orr & Turelli 2001; Coyne & Orr 2004; Gavrilets 2004; Dettman *et al.* 2007). The underlying logic is that genes within a population are tested to work well together, whereas genes from different populations have not been tested together. Thus, alleles that are advantageous (or neutral) within populations might be incompatible when combined in between-population hybrids. Under this class of models, increased genetic divergence translates to increased probability of genetic incompatibilities, and higher likelihood of speciation (see Orr 1995 for details). For example, a first substitution

Figure 8.5 The effects of dimensionality of fitness landscapes on the fitness of hybrids relative to parental taxa. (a), total fitness is determined by the independent effects of an increasing number of loci which are each under selection; at each locus, heterozygote fitness is equal to 80% of the parental homozygotes. In (b) and (c), populations evolving on a fitness landscape are considered; in (b), peaks differ in their position along only one phenotypic axis (x ; -4 and 4 ; $y = 0$); in (c), peaks differ in their position along both the x and y axes. (d) compares the shape of the fitness surface along a straight line connecting both peaks in (b) and (c). To investigate hybrid fitness, simulations were conducted using the software Nemo (Guillaume & Rougemont 2006). For each simulation, two populations were created. Each population was made up of 10 000 individuals whose traits were determined by 50 unlinked loci. Mutations occurred at a low rate (0.0002) and had pleiotropic effects on all traits; mutational effects were drawn from a multivariate normal distribution with mutational variance $\sigma_m^2 = 0.05$ for each trait and zero expected genetic covariance among traits. Thus, each of the 50 loci contributed to all of the phenotypic traits. Populations were evolved for 10 000 generations, at which point mean fitness and genetic variances had stabilized due to mutation-selection-drift equilibrium. The fitness surface was described by two peaks, each determined by a multivariate normal distribution with variance of four and no selective covariance among traits. Hybrids were formed by drawing one parent from each population. For one set of simulations (e), the populations evolved on multidimensional fitness landscapes similar to (c), where peaks differ at their position along all axes. In another set of simulations, (f), peaks on the fitness landscape with peaks differing only along one axis ('Phenotype 1'; b). These simulations show the effects of the number of traits pleiotropically affected by mutations on the fitness of hybrids relative to parental taxa.

at locus A cannot cause a between-locus incompatibility, a second substitution at locus B might cause one incompatibility (with locus A), a third substitution at locus C might cause two incompatibilities (with A and B), and in general the Kth substitution can be incompatible with K-1 loci. Thus for incompatibilities between pairs of the loci, the number of incompatibilities increases with the square of the number of substitutions (Orr 1995). For complex incompatibilities involving three or more loci, the rise of the number of incompatibilities with the number of substitutions is even faster. The Dobzhansky-Muller model generates the prediction that increased dimensionality in niche divergence promotes speciation if the following assumption is made: as dimensionality in niche divergence increases, genetic divergence between populations (i.e. number of substitutions separating them) increases.

Models invoking magic traits or linkage disequilibrium

In another class of models, genes under divergent selection have a pleiotropic effect on forms of reproductive isolation such as mate or habitat preference ('single-variation' models of Rice & Hostert 1993, 'direct selection' models of Kirkpatrick & Ravigné 2002, 'no-gene' models of Coyne & Orr 2004, 'magic-trait' models of Gavrilets 2004). Speciation via this mechanism might become more likely as the dimensionality of divergence increases, because as niches become divergent in more dimensions, more traits differ between taxa, and genetic divergence in the key genes (traits) that incidentally affect reproductive isolation becomes more likely. A similar argument could apply to models using the build up of linkage disequilibrium between selected and reproductive isolation loci (Felsenstein 1981; Kirkpatrick & Ravigné 2002; see Gavrilets 2004 for review); when dimensionality increases, the probability that a gene involved in adaptation will be in linkage disequilibrium (e.g. physically linked) with a gene involved in reproductive isolation might increase. In general though, there is not much explicit theoretical work relating niche dimensionality to speciation. Thus further theoretical work, particularly work focusing on analytical theory and macro-evolutionary models (see Gavrilets & Vose 2005 and this volume), could be fruitful.

Alternatives summarized: many genes or the right genes?

The alternative mechanisms noted above can be divided into two main classes: those that invoke divergence in a greater number of genes that each more or less equally affect reproductive isolation (e.g. genetic dimensions and ecological selection against hybrids) and those that invoke a greater sampling of the genome such that divergence is more likely in the few key genes affecting reproductive isolation (e.g. Dobzhansky-Muller and Magic Trait models). These can be thought of as 'accumulative' and 'sampling' models, respectively. An analogy can be drawn with the association between ecosystem function

(e.g. productivity, nutrient cycling) and species diversity: does this association arise because a greater number of more or less equally important species better fills ecosystem requirements, or because greater species number increases the probability that a few key (e.g. keystone) species are represented within the ecosystem (Hooper & Vitousek 1997; Tilman *et al.* 1997)?

Niche dimensionality and peak shifts during speciation

Throughout this article we have implicitly assumed that populations will reach different peaks in the adaptive landscape, and thus that the major problem of speciation is the build up of reproductive isolation, particularly in the face of homogenizing gene flow (see Bridle & Vines 2006, this volume; see Gavrilets & Vose, this volume, for consideration of the limits to adaptation and the costs of gene flow when divergence is multidimensional). In contrast, it has been argued that peak shifts themselves are a central problem for speciation, because large peak shifts are difficult, but small ones result in only weak reproductive isolation (Wright 1932; Barton & Rouhani 1987; Fear & Price 1998; Gavrilets 2004; but see Whitlock 1997). It could be that large valleys between peaks in a single dimension do not generate speciation because they cannot be crossed. In contrast, with many dimensions each separated by a smaller valley, perhaps each dimension can be crossed, gradually building up reproductive isolation as more dimensions are adapted to.

Alternatively, by increasing separation between peaks, increasing niche dimensionality might decrease the probability of peak shifts (but increase the probability of speciation should those valleys be crossed). Additionally, peak shifts might be further affected by frequency-dependent selection. For example, niche dimensionality might start out low, with a narrow valley that can be crossed in a single dimension. As adaptation proceeds, species interact in new ways, thus gradually building up niche dimensionality (and the potential for reproductive isolation) among different sets of adaptive characters (Streelman & Danley 2003). Thus, if peak shifts are a central issue in speciation, a correlation between dimensionality of niche divergence and speciation might be expected, but only under certain scenarios. The net outcome of these counteracting forces is unclear, and deserves further study.

Causality and the role of time since divergence

A final issue to consider is causality. Not only can gene flow decrease (i.e. reproductive isolation increase) with increasing dimensionality of niche divergence, but, conversely, the dimensionality of niche divergence can grow with decreasing levels of potentially homogenizing gene flow. Thus when it comes to an association between dimensionality of niche divergence and levels of gene flow, it may often be difficult to determine the direction of causality. Moreover, a feedback loop can exist between the two processes, such that niche divergence

reduces gene flow, which then allows further niche divergence, which then further reduces gene flow, and so on (Hendry & Taylor 2004; Nosil & Crespi 2004). A minimum dimensionality of niche divergence could be required for divergent selection to be sufficiently strong to initiate speciation, but once gene flow becomes sufficiently reduced, divergence in other traits that are under weaker selection becomes possible (Strelman & Danley 2003). Such a scenario might be occurring in the African cichlids studied by Seehausen and colleagues (Seehausen, this volume).

The issue of causality further raises the question of the role of time since divergence. It is accepted that time since divergence is positively related to the degree of progress towards speciation (reviewed in Coyne & Orr 2004). It could be that adaptation to a greater number of niche dimensions requires more time than adaptation to one or a few dimensions. In that case, a critical role for time in speciation could arise through the association between time and dimensionality of niche divergence. Alternatively, the dimensionality of niche divergence could be positively related to the degree of progress towards speciation independent of time. In this case, population pairs of equal age that differ in the dimensionality of their niche divergence would differ in their degree of progress towards speciation. In both scenarios, dimensionality of niche divergence could play a role in speciation, but with time sometimes playing an important role and sometimes not. The types of reproductive barriers involved might determine whether time plays a role. For barriers that evolve quickly and early in the speciation process (e.g. premating isolation), the dimensionality of niche divergence may play a role independent from time, whereas for more slowly evolving barriers (e.g. intrinsic incompatibilities) a role for time may be more likely. Empirical data are required to determine the incidence of these scenarios.

Conclusions

Divergent selection between niches can promote speciation. However, often progress towards ecological speciation is incomplete, or species pairs collapse. A number of ecological, genetic and geographic factors might explain the degree of progress towards complete speciation, and the maintenance of species. The focus here was on whether dimensionality in niche divergence affects speciation. Although existing information is suggestive of a potential role for such divergence, direct data are almost completely lacking. Once more definitive evidence for a positive association between dimensionality in niche divergence and speciation is established, it will be of interest to determine causality, and to distinguish among the alternative mechanisms generating the association.

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