

Species selection in the molecular age

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Introduction

Everything biological varies. Without variation, evolution would not be possible. This is a truism in macroevolution as much as it is within and between organisms. Species vary in their phenotypic and macroecological traits (Brown 1995) and variation also exists in the taxonomic rates of speciation and extinction over time (Alroy 2008), among taxa (Van Valen 1973; Sepkoski 1981; Raup and Boyajian 1988), and within taxa (Van Valen 1973, 1975; Liow *et al.* 2008; McPeck 2008; Simpson and Harnik 2009; Simpson 2010). Variation in diversification rates produces the major patterns of diversification we observe in the fossil record. Understanding the patterns and causes of variation in diversification rates has been the focus of palaeobiology for decades (Simpson 1944, 1953; Van Valen 1973; Raup 1978; Gould and Calloway 1980; Sepkoski 1981; Raup 1991a, 1991b).

Palaeobiologists, however, are not the only ones interested in understanding the patterns and causes of diversification. Diversification is also interesting to ecologists for at least two reasons. Major spatial patterns of diversity such as the latitudinal diversity gradient are likely to be underpinned by historical patterns of speciation and extinction (Jablonski and Hunt 2006; Krug *et al.* 2007, 2008; Kiessling *et al.* 2010). Also, many distributions of ecologically important traits, for example body size, may be, in part, a product of the historical patterns of differential diversification (Stanley 1975; Van Valen 1975). The second interest is the issue of diversity limitation. Data from the fossil record and molecular phylogenetics of extant organisms have been brought in to study this issue and evidence is accumulating that diversity is, in fact, constrained (Cracraft 1982; Nee *et al.* 1992b; Paradis 1997; Pybus and Harvey 2000; Nee 2001; Ricklefs 2007; Alroy 2008, 2009, 2010; Alroy *et al.* 2008; McPeck 2008; Phillimore and Price 2008; Rabosky and Lovette 2008a, 2009b; Phillimore and Price 2009; Quental and Marshall 2009, 2010; Rabosky 2009b).

Given the many ways that rates vary, we know little about the causes of diversification rates. While proponents of the concept of 'constrained diversification' argue for ecological control (Alroy 2008), variation in rates within and among taxa could also be caused by morphological traits. The fact is that the causes of diversification rates will be many, variable, and possibly nonlinear, and this multivariate complexity makes synthesis difficult. But there is a way to cut through the complexity. Variation in diversification rates creates the potential for evolution to occur at or above the species level due to species selection.

Species selection occurs when there is a causal relationship between a trait and fitness, which in species selection is diversification rate. In multilevel selection, and species selection in particular, there is more than one level of fitness (Arnold and Frisrup 1982; Jablonski 2008; Simpson 2010). Fitnesses that occur at hierarchical levels above the familiar organismal level, such as the colonial, are understood in general detail (Simpson 2011, 2012). But in species selection there are levels of demography – speciation and extinction – that constitute higher-level fitness. In species selection, the traits themselves need not even be expressed at the organismal level. So in contrast to a phenotypic trait relevant to the fitness of an individual, higher-level fitness traits can also be emergent, expressed only at higher hierarchical levels and not reducible to organismal traits. Much of the discussion of species selection has focused on these definitions (see Grantham 1995 for a review). However, as we will see below, species selection can simply be understood as the causal covariance between traits (at any level) and diversification rates (which is a higher-level fitness).

If selection is to occur, a simple mathematical relationship between fitness and causal traits must be obeyed. This theorem, known as the Price's theorem, is an exact description of evolutionary change over time, and is particularly useful if multiple levels of selection co-occur (Hamilton 1975; Arnold and Frisrup 1982; Rice 2004; Okasha 2006; Rice 2008; Simpson 2010). The change in the mean of a trait over time can be decomposed into the change attributable to the process of natural selection and the change attributable to the process of reproduction (which includes selection at lower levels and a multitude of other processes). The magnitude and direction of selection (S) is a function of the covariance between phenotype (ϕ) and fitness (W): $S = \frac{1}{W} \text{cov}(W, \phi)$, or equivalently as a function of the linear regression of fitness on phenotype and the variance in the phenotype $S = \frac{1}{W} \beta_{\phi, W} \text{var}(\phi)$ (Rice 2004). The fact that the important relationship between fitness and phenotype is simply their linear regression makes the empirical detection of species selection straightforward because any nonlinearities in the relationship between traits and diversification

rates can safely be ignored (Simpson 2010). The covariance approach to species selection also helps clarify how multiple traits may evolve by species selection given the covariation among traits and their heritability (Rice 2004; P. G. Harnik *et al.* unpublished data).

Species selection has a long conceptual history (Gould 2002; Jablonski 2008) going back to Lyell (Lyell 1832; Van Valen 1975). Within palaeobiology, species selection was largely discussed and accepted as a hypothetical evolutionary process with the ability to be an effective force contingent on the pattern of punctuated equilibrium (Gould 2002). Gould and others used the pattern of punctuated equilibrium as a way to derive species selection through the process of elimination. If there is a trend in a clade, and species within the clade are static over time, then one possible way to reconcile these patterns is if diversification rates varied in such a way as to produce the trend. Gould (2002) bundled together species selection and punctuated equilibrium largely to deal with Williams' (1966) criticism of group selection. Williams argued that group selection could only be invoked if other selective forces are opposing or have zero strength. Although it is easier to think about species selection when punctuated equilibrium occurs, there is no need for restricting the operation of species selection to those scenarios (McShea 2004; Jablonski 2008; Simpson 2010). This is because speciation and extinction can co-occur with the birth and death of organisms. As a consequence, the species-level selective vector can also co-occur with the organismal-level selective vector and they can have any angle between them (Slatkin 1981; Arnold and Fristrup 1982; Rice 1995; Simpson 2010). Species selection is still largely an open empirical issue – we do not know its relative frequency, how strong it can be, or what sorts of traits may evolve due to its action.

Many discussions of species selection focus on the types of traits that cause differential diversification rates. Two basic types of traits are discussed: organismal-level and emergent traits. Often species selection (in the strictest sense) has been restricted to those times where differential diversification rates are caused only by traits that are emergent at the same level (Grantham 1995; Jablonski 2008). Emergent traits cannot be expressed in the phenotype of a single organism, as they are properties of populations of organisms. The majority of these traits are macroecological: geographic range, abundance, and population structure are good examples. Other traits, like body size or dispersal ability are somewhat unclear if they are emergent since they can influence diversification rates and organismal-level fitness (Van Valen 1971, 1975). Traits like body size illustrate the importance of not restricting species selection to being caused by only emergent traits a-priori – diversification rates may be caused by traits at any hierarchical level. The only requirement for the operation of species selection is that differential diversification rates are caused by some (biotic or abiotic) factor.

Many palaeontologists have suggested that large-scale morphological trends have been caused by species selection so that traits change in frequency over time due to their covariance with diversification rates (Arnold and Fristrup 1982; Vrba 1984; Vrba and Gould 1986; Gould and Eldredge 1988; Lloyd and Gould 1993; Grantham 1995; Gould and Lloyd 1998; Gould 2002; Okasha 2003; McShea 2004; Jablonski 2008). Adaptive, organismal-level explanations for these trends are not possible because the trends occur over such vast amounts of time, and organismal-level selection must surely fluctuate. However, some recent empirical work on the subject has found that the effect of species selection is not uniform either, at least during a large-scale trend in crinoid morphology (Simpson 2010). Not surprisingly, the pattern of selection varies in both magnitude and direction over the history of crinoids in a way very similar to the fluctuations observed in selection in recent organisms (Grant and Grant 2002). Fluctuating selection makes sense both biologically and in light of large-scale trends; trends are not common across taxa nor are they generally persistent when they do occur. The strategy of identifying species selection only in trends will tend to miss many examples of real species selection.

Time-calibrated molecular phylogenies are a potentially rich source of data on the species selection that has not been explored to its full potential (Rabosky and McCune 2009). But species selection has always been of interest to those working on diversification in molecular trees (Nee *et al.* 1992b). The major strategy most of this work uses is to develop models of the evolutionary process that can then be fit to the patterns of species diversification, usually in the form of various types of branching models (Nee *et al.* 1992a, 1994; Nee 2001, 2004, 2006; Maddison *et al.* 2007; Ricklefs 2007; McPeck 2008; Phillimore and Price 2008; Alfaro *et al.* 2009, 2010; FitzJohn *et al.* 2009; Quental and Marshall 2009, 2010; Rabosky 2009a, 2009b; FitzJohn 2010). An example is the Yule model, a time-homogeneous pure-birth branching process. In this model, speciation rate is constant and there is no extinction. Additional complexity is incorporated in the birth–death processes, which factors extinction into the Yule model. Variations in diversification rates are identified either temporally (Simpson *et al.* 2011) or by looking for variations in species richness or character state that indicate rate shifts (Maddison *et al.* 2007; Alfaro *et al.* 2009, 2010; FitzJohn *et al.* 2009, 2010).

Our goal in this chapter is to reboot the discussion of inferring diversification from molecular phylogenies with the goal of establishing not only the potential for identifying temporal variation in rates in a molecular phylogeny, but also its causes. The full potential of studying species selection is more than conceptual; the simple pattern of selection provides an easy entry into the complex interaction between traits and rates. We focus our attention away from how to use various branching models towards the statistical description

of rate variation. Additionally, we use Price's theorem to interpret variations in diversification rates biologically. We will illustrate a macroevolutionary-minded way to construct temporal patterns of diversification. An additional issue, about the pattern of covariance between taxonomic rates and phenotypic or macroecological traits, opens the door to answering an important macroevolutionary question – what factors control the rates of diversification?

Measuring speciation and extinction rates

It is standard practice in palaeobiology to estimate time series of taxonomic rates from only those species or genera that are observed to cross a temporal boundary between stages or other temporal bins. Estimating boundary crosser rates (Foote 2000; Alroy 2008; Alroy *et al.* 2008) involves tabulating the numbers of four fundamental types of taxa: (1) the number of taxa that both enter in and cross out of an interval, N_{bt} ; (2) those that enter in and go extinct in the interval, N_{bL} ; (3) those that originate in the interval and cross out of it, N_{Fi} ; and (4) the taxa that are restricted to the interval, N_{FL} . Of these four types of taxa, only three are used to estimate rates. Maximum likelihood origination rates (\hat{p}) are a function of the number of taxa that cross through an interval and the number originating there: $\hat{p} = -\ln(N_{bt}/N_t)$, whereas extinction rates (\hat{q}) are a function of the number of taxa crossing through an interval and entering into it: $\hat{q} = -\ln(N_{bt}/N_b)$ (Foote 2003; Kiessling and Aberhan 2007). These rates are derived from an exponential model, where the probability of a lineage leaving an interval that was already extant at the start is: $N_{bt} = N_b e^{-qi} = N_t e^{-pi}$ (Foote 2003).

Although these 'boundary crosser' rates are thought to be equivalent to those that are calculated from molecular data (Nee *et al.* 1992b; Alroy 2009), there is a tendency for boundary crosser rates to be much larger than rates estimated only from molecular data alone. This is due to the fact that counts of one (N_{bL}) of the three fundamental types of taxa used to measure rates cannot be made in molecular phylogenies. This makes direct estimation of extinction rates impossible and also biases estimates of speciation rates. If taxa that contribute to N_{bL} in one interval are long lived, they will not be able to contribute to N_{bt} in prior intervals in which they range through either.

Simpson *et al.* (2011) proposed a new method for estimating diversification rates from molecular phylogenies and results in a time series of rates. Given a phylogeny, diversification rates within an interval of time can be estimated from the number of branching events (k_i) and the sum of branch lengths in the interval – including branches that range through without speciating. The number of lineages ranging through, but not branching, is equal to the total number of lineages in the interval, n , minus the number of

branching events, k_i , or $n - k_i$. Note that branching event i occurs at time t_i . The time span represented by each stage is denoted Δt_i and the youngest age of the stage is denoted t_i . The maximum likelihood estimator of diversification rate is equal to

$$\bar{\delta} = k_i / \left[(n - k_i) \Delta t_i + \sum_{i=1}^{k_i} (t_i - t_j) \right].$$

Repeating this equation over time intervals, such as geological stages, provides a time series of rates directly comparable to rates estimated from the fossil record. Using this approach, Simpson *et al.* (2011) found a significant positive correlation between changes in diversification rates estimated in fossils and molecular phylogenies in reef corals (see also Larsson *et al.*, this volume, for a comparison of morphological rates of evolution against those derived from molecular studies).

Despite this high correlation in pattern, the magnitudes of the molecular diversification rate estimates are biased by the lack of species that contribute to N_{bt} . This bias means that speciation and extinction rates cannot be meaningfully estimated directly from molecularly derived phylogenies of only extant species (Simpson *et al.* 2011). But because the trajectory of those rates is robust, any differential rates of diversification can also be inferred. This ability to measure differential rates allows species selection to be studied using molecular phylogenies.

Detecting species selection

All species selection is a covariance between diversification rates and various traits that a species or members of a species possess (Simpson 2010). There are two major possibilities for how this covariance can occur. The first is that variation in rates can be largely random and uncaused. This would result in drift at the species level if some minor phenotypic change accumulated (Gould 2002). Species-level drift (a higher level version of drift in microevolution) is particularly important if the number of species is small. This is because chance events, such as the survival of one species with a particular set of traits, will over time have a large effect on the frequency distribution of those traits in the species pool. On this basis, Gould (2002) argued that species drift may be common in the history of life because the numbers of species involved are low. But species drift may actually be relatively rare if trends are uncommon and heritability of macroecological traits is high (Jablonski 1987; Hunt *et al.* 2005), because some selective vector would be needed to oppose any morphological change due to correlations with macroecological traits (P. G. Harnik *et al.* unpublished data).

The covariance between diversification rate and traits may also be causal. Many macroecological traits correlate with extinction and speciation rates (Jablonski 1987; Payne and Finnegan 2007; Simpson and Harnik 2009; Simpson 2010) and many workers consider these traits to be causally linked even if the actual causal pathways remain unknown. Macroecological traits often covary with each other (Brown 1995) and with extinction (Purvis *et al.* 2000) in complex ways, so trends in macroecological traits are not expected to produce trends consistently. This complexity of causes provides us with an opportunity to use species selection and the predictive ability of Price's theorem as entry point to discovering and untangling the causes of evolutionary rates.

It has often been argued that tree asymmetry (where some basal branches are species poor and others are species rich) is diagnostic of species selection (Lieberman *et al.* 1993; Rabosky and McCune 2009). But this is not true, as it has been shown that changes in character states can influence diversification even if these traits are sprinkled throughout a phylogeny (Maddison *et al.* 2007; FitzJohn *et al.* 2009; FitzJohn 2010; Simpson 2010). Species selection is a process that is independent of tree topology, but many possible traits may still have characteristic qualitative patterns detectable from the distribution of traits on trees alone. From this point of view, there are three possible ways that species selection can occur (Figure 5.1). (1) Species selection can occur among higher taxa if divergences among their traits cause differences in their diversification rates. (2) Species selection can occur within higher taxa when a monophyletic subclade differs in rates from other subclades. (3) But species selection can also occur among unrelated members of a higher taxon that share the same trait values. In analogy with organismal-level selection, what matters for fitness is the trait value of individuals, not their pedigree. If large bears have more offspring, even large bears from small parents will have more offspring. Now at the species level, if large geographic range prevents extinction, it does not matter if a species is descended from a small-ranging parent.

The only thing that distinguishes between these three forms of species selection is how the causal traits vary across the phylogeny. In the first type, traits are invariant within a taxon but vary among them. In the second type of species selection, a monophyletic clade within a higher taxon possesses a trait which then influences diversification. An extreme example of this would be when a key innovation causes an adaptive radiation, where high rates are associated with the evolution of a single trait. Macroecological traits, however, are much more variable and so may commonly underlay the third type of species selection. Not only do all taxa share traits (for example, every species has a geographic range), but often species with a particular macroecological trait,

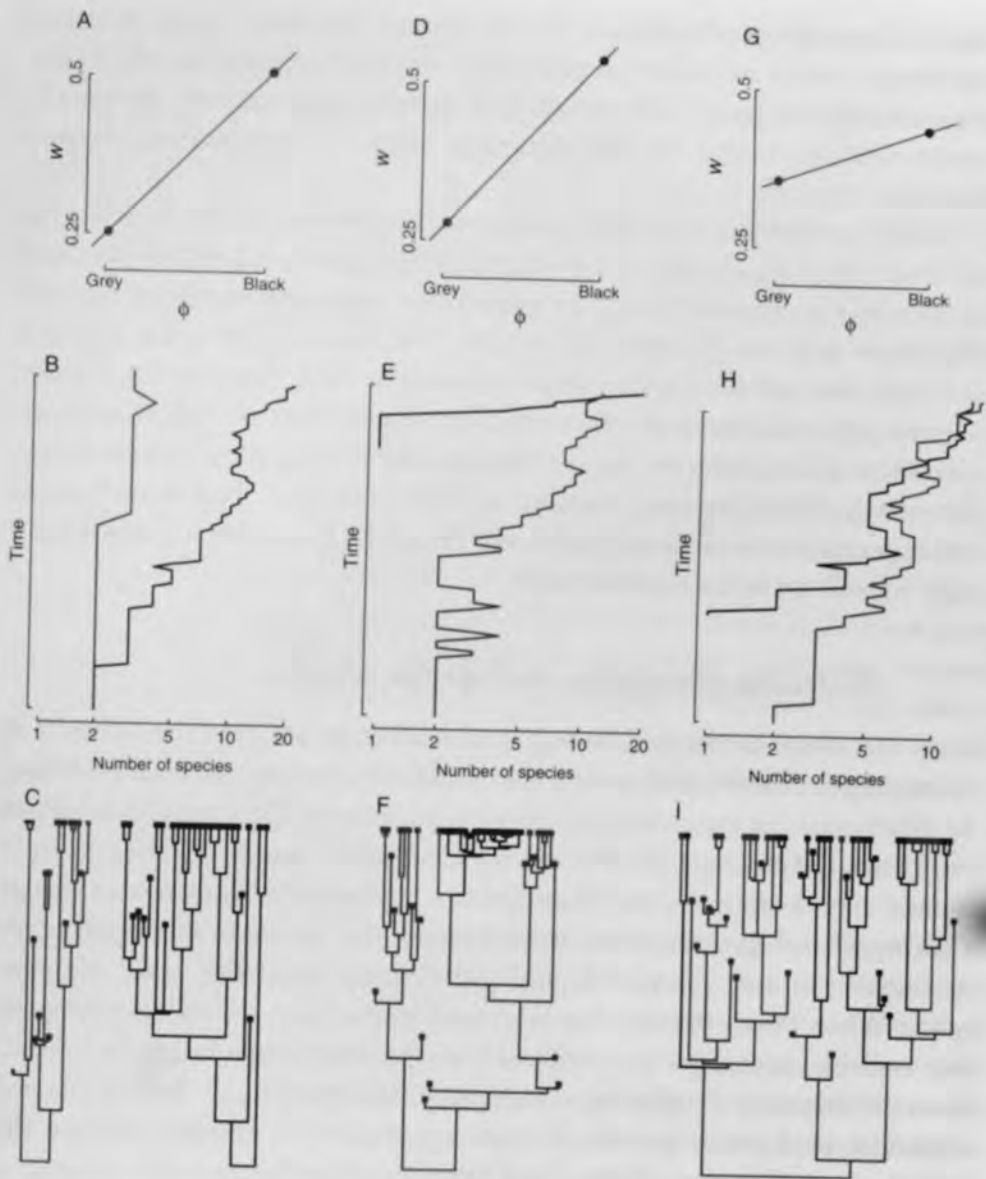


Figure 5.1 Three types of species selection distinguished by the distribution of traits across a phylogeny. In all panels, the black group has higher diversification rates than the grey group. In the first column (panels A, B and C), traits are invariant within clades but vary among them. The middle column (D, E and F) shows species selection where a single clade has a higher rate of diversification than the rest of the clade. And the right column (G, H and I) shows species selection where the high diversification trait is distributed across the tree. The diversity over time for the high and low rate groups are plotted for each type of species selection (B, E and H). The selection gradient for each type of species selection is shown in the top panels (A, D and G). Note that from the point of view of selection, each type of species selection is equivalent.

such as large geographic range, are not directly related. If macroecological traits were used for taxonomic purposes, then membership would be polyphyletic. As a consequence, groups with members of mixed ancestry are not a problem for species selection because the only thing that matters is the covariance between traits and rates.

Unfortunately there is no ideal solution to the problem of how to detect rate variation within a clade. A recent inverse modelling approach has been developed to identify the effects of binary or quantitative characters on taxonomic rates (Maddison *et al.* 2007; FitzJohn *et al.* 2009; FitzJohn 2010), but this approach, as of yet, does not allow for temporal variation in rates. Alternatively, a model selection approach has been used successfully recently that identifies time intervals where differential rates occur (Simpson and Harnik 2009; Simpson 2010; Simpson and Kiessling 2010; Kiessling and Simpson 2011). This second, model selection approach is easily integrated into Price's theorem (Simpson 2010) and is what we will use in the example below.

Molecular phylogenies and species selection

A major hurdle to detecting species selection has been the difficulty in untangling alternative mechanisms that could influence species-level evolution, for which stasis (or punctuated equilibrium) has been seen to control (Lieberman *et al.* 1993; Gould 2002). Price's theorem approach to species selection helps to unravel it from other processes that lead to a phylogenetically correlated change (like organismal-level selection) by partitioning the change in mean phenotype attributable to each process (Arnold and Fristrup 1982; Rice 2004; Simpson 2010). When Price's theorem has been used in the fossil record, no phylogeny was available, so changes not attributable to species selection had to be inferred from the frequency distribution of phenotypes (Simpson 2010). Time-calibrated molecular phylogenies provide the best opportunity to directly measure the contribution of species selection and other processes because they contain a record of both rate variation and phylogenetic relationships.

Let us now focus on one specific example: the evolution of pharyngeal jaws in labrid fishes (Alfaro *et al.* 2009). Modifications to the pharyngeal jaw apparatus are thought to be a key innovation (see Smith and Johanson, this volume) that drives high diversification within the labrids (Liem and Greenwood 1981; Kaufman and Liem 1982; Stiassny and Jensen 1987). Alfaro *et al.* (2009) found that a subsequent diversification of parrotfishes is associated more strongly with diversification driven by sexual selection in the *Scarus-Chlorurus* clade than with the evolution of the parrotfish pharyngeal mill. We can demonstrate the utility of Price's theorem approach to species selection by reanalysing the labrid data.

Although we largely replicate the results presented in Alfaro *et al.* (2009), we can take the analysis one step further by identifying if it is sexual selection or jaw structure that influences diversification within the parrotfish lineage to a greater extent.

The simple Price's theorem formulation of selection described above is for only a single trait, but it can easily be extended to a multivariate situation. Recall that the selection differential (S) is defined, $S = \frac{1}{\bar{W}} \text{cov}(W, \phi) = \frac{1}{\bar{W}} \beta_{\phi, W} \text{var}(\phi)$. Incorporating multiple traits involves measuring the linear regression of fitness on each trait independently with its partial regression, $\beta_{\phi_i, W}$, where ϕ_i indicates variation in trait i that is independent of other traits. This can be done using multiple regression or path analysis depending on what underlying model of covariation among traits we are interested in. This results in one partial regression on fitness per trait (in the vector, $\vec{\beta}_{\phi, W}$) and therefore a vector (\vec{S}) represents selection in all traits. If the variance-covariance matrix of traits is denoted P , then the multivariate selection vector is equal to: $\vec{S} = \frac{1}{\bar{W}} P \cdot \vec{\beta}_{\phi, W}$ (Rice, 2004). In labrid fishes, the parrotfish pharyngeal jaw mill does not cause sexual dichromatism (which is a colour difference between the sexes) because sexual dichromatism is not limited to the parrotfishes. If there is a tight association, then a causally explicit path model could be used to specify the partial regressions in $\vec{\beta}_{\phi, W}$. Instead, we use a simple multiple regression approach to capture the covariation between our traits of interest.

A temporal pattern of diversification rates is estimated using the method of Simpson *et al.* (2011), which we outlined above. In Figure 5.2 we present a time series of selection gradients for the parrotfish pharyngeal mill and sexual dichromatism. On average, selection is much stronger for sexual dichromatism ($\bar{S}_{SD} = 0.279$) than for jaw structure ($\bar{S}_{PPM} = 0.016$) when controlled for their covariance. From the magnitude of the selection coefficients, we can infer that sexual dichromatism and sexual selection played a considerably larger role in parrotfish diversification than did their innovative jaw mechanism. Relative to other labrid fishes, selection is actually against the parrotfish pharyngeal mill for a period of approximately 10 million years in the Miocene (Figure 5.2). This decline in relative diversification rates occurs near the time when modern coral-algal reefs start to decline in volume from their early Miocene peak (Kiessling 2009).

Controlling for the covariance between traits makes a difference in the inferred patterns of diversification. In Figure 5.2 there is a peak in the diversification rate of species with the parrotfish pharyngeal mill in the early Miocene that is not seen in the selection coefficients. When covariance between jaw structure and dichromatism is taken into account, the diversification rate of the parrotfish is relatively lower than the rates for the clade with sexual

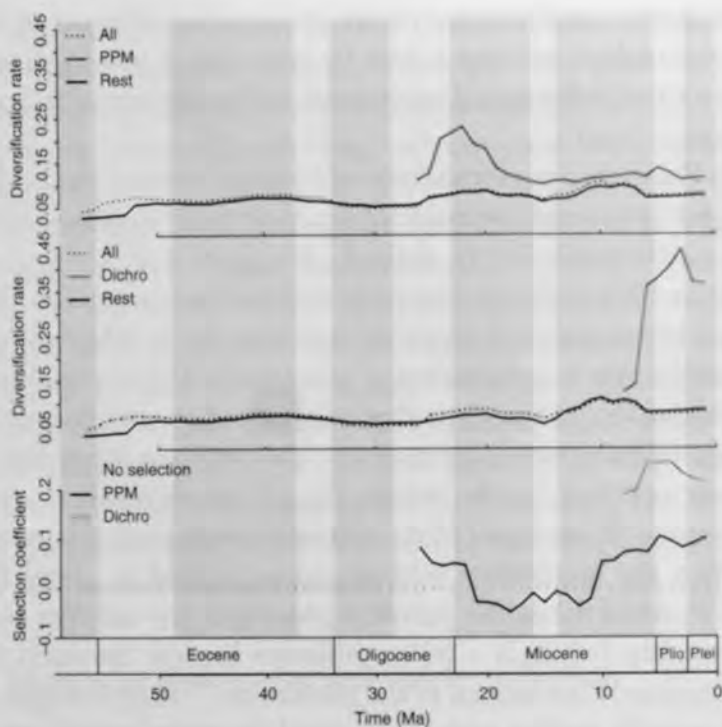


Figure 5.2 Temporal patterns of diversification in labrid fishes. Branching lengths are partitioned into those with and without parrotfish pharyngeal mills (top panel) and those with and without sexual dichromatism (middle panel). Model averaging is used to estimate diversification trajectories from a pool of four models (see text for discussion). A model selection approach is then used to test if a two-rate model (where rates differ between lineages with each character state) is supported over a single-rate model independent of character state. In both plots, the dotted line is the diversification rate for all labrids. Estimates of selection coefficients (bottom panel) for jaw structure and sexual dichromatism in labrid fishes over time. Selection coefficients are estimated from the diversification rates in the top panels and account for any covariance between jaw structure and sexual dichromatism.

dichromatism and so the Miocene peak is tempered. Converting to relative rates and controlling for the covariance among traits allows us to compare the selection acting on individual trait states. The parrotfish jaw is temporarily selected against, which means that relative to the rest of the labrids, parrotfish diversify at a comparatively lower rate.

Sexual dichromatism may not directly increase diversification rates. If not, some other character that is precisely codistributed with it must. This may sound unsatisfying at first, but the fact that we know that the trait causing

high rates in parrotfish is codistributed with sexual dichromatism, means that many potential characteristics can be rejected outright once they are mapped onto the phylogeny if they do not vary with sexual dichromatism. In the worst case, the cause of selection is just a correlation away.

How common and strong is species selection?

Now that we know that species selection is the variation in diversification rates within a clade, we can ask an important question: What is the relative frequency and average strength of species selection in nature (Jablonski 2008)? Using molecular phylogenies, we can provide an approximate answer by looking for an indicator of species selection. In the simplest case, if species selection operates within a clade, then the frequency distribution of branch lengths of that clade will be the result of a composite of many diversification rates. If rates vary among character states, then there will be one rate per state. One problem with measuring the relative frequency of species selection is that the phenotypic groupings are unknown a-priori. Binary, multistate or quantitative characters may cause species selection so the number of groups in a clade (and thus the number of different rates within it) is unknown prior to analysis. What we can measure a-priori – and without knowing the causal traits – is the variance in rates within a clade. A simple way to measure the variance among all the potential groupings is to estimate the inverse of the shape parameter ($1/\alpha$) of the gamma distribution (Holman 1983; Venditti *et al.* 2010; C. Simpson, unpublished data) fit to the distribution of branch lengths in a clade. The benefit of this approach is that the variance in the rates can be estimated without defining the number or identity of groups. If there is no variation in rates within a clade, the gamma distribution becomes equivalent to an exponential, so there is no tendency to find rate variation if there is none present. Multiple rates are inferred to be present if $1/\alpha > 0$ and their variance is given by $1/\alpha$. This is an indirect test so may be confounded by other processes such as the temporal variation of rates of the group as a whole without species selection. A non-zero variance is only necessary for species selection, not sufficient. If we find zero or small variances, there is little chance for species selection to operate. Keep in mind that with this approach we can reject the operation of species selection in cases where variances in rates are small, but not prove its operation in those cases where the variance is high. A non-zero variance indicates that the raw material for species selection, variation in rates, is present.

In order to empirically investigate this issue we used the set of 245 time-calibrated trees of chordates, arthropods, molluscs and plants compiled by

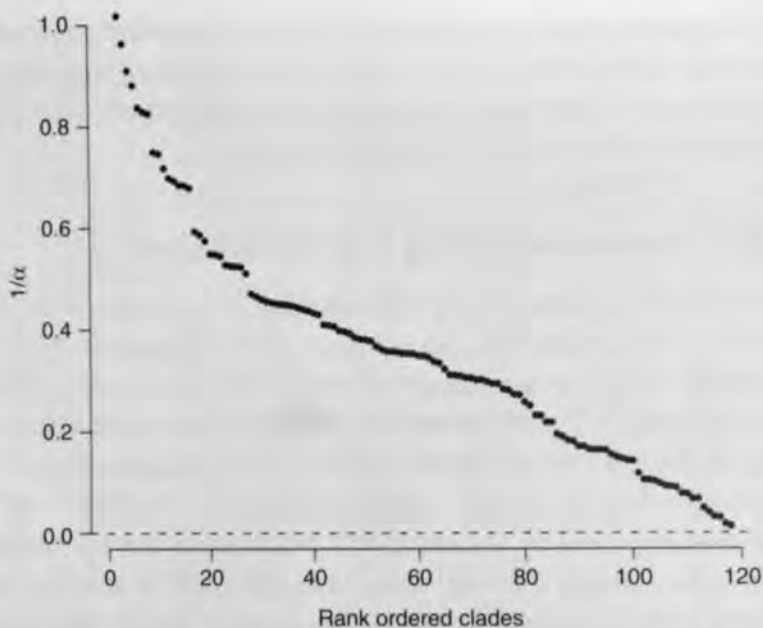


Figure 5.3 The inferred necessary conditions for species selection in time-calibrated molecular phylogenies of extant organisms. If a clade diversifies with more than one rate, the shape parameter ($1/\alpha$) of the gamma distribution will estimate the variance of the constituent rates, which measures the strength of species selection. The greater the variance in rates, the stronger the selective vector will be. Plotted here in rank order is the variance in diversification rate of chordates, arthropods, molluscs and plants derived from 120 time-calibrated molecular phylogenies (data from McPeck 2008 and McPeck and Brown 2007). The raw material for species selection is inferred to operate within clades when $1/\alpha$ is larger than zero. If there is only a single rate, and consequently no species selection, $1/\alpha$ will be equal to zero and equivalent to an exponential distribution.

McPeck (McPeck 2008; McPeck and Brown 2007) as an example. By applying non-parametric rate smoothing (Sanderson 1997) we convert the trees into ultrametric chronograms and then scale the branch lengths to units of time following the calibration protocol of McPeck and Brown (2007).

Out of the 245 trees in the data set, we were able to estimate a shape parameter ($1/\alpha$) for 118 clades. We found that 100% of the clades have a non-zero variance, suggesting that the raw material for species selection is ubiquitous in these clades (Figure 5.3). Our result is not surprising given that rate variation among clades has been long observed, with each higher taxon having its own rate (Van Valen 1973; Sepkoski 1981; Raup and Boyajian 1988; Alroy 2004, 2008). However, until we have an estimate of the relative importance of macroecological or

morphological traits, we will be unable to know what the most common cause of species selection is. Even so, we can conclude that species selection in some form is ubiquitous in nature, both within and among clades.

Conclusions

Species selection is not just of theoretical interest to palaeobiologists. It can be used to cut through complex interactions between traits and rates to identify each trait's relative contribution to diversification. As we were able to show, Price's theorem is a powerful way to organize measurements and to help ask the right questions about the causes of evolutionary rates. Also, it is the temporal pattern of selectivity that is the key to identifying the traits that cause species selection. In our example, the labrid fishes, it is sexual selection that inflates diversification rates consistently and strongly. In comparison, the parrotfish pharyngeal jaw apparatus can be rejected as a direct cause of high diversification because its association with diversification rate is variable in magnitude and direction. Although it is clearly an important trait, diversification is not directly caused by its presence.

When measured temporally, the magnitude and direction of species selection on organismal-level traits varies widely (Figure 5.2 and Simpson 2010). Conversely, many emergent traits, such as sexual selection (as it is the resultant of interactions among organisms) and geographic range, have been observed to be associated with species selection that is consistent in direction but variable in magnitude (Figure 5.2 and Payne and Finnegan 2007). It is too early to tell if this is a general result, but the inference we can make from these patterns is that emergent traits may be more important for diversification than organismal-level traits.

The question about the relative frequency and strength of species selection can, however, be made without knowledge of the number or kind of traits involved. The variance in rates, estimated by the shape parameter of a gamma distribution fit to the distribution of branch lengths, is positive in a broad sample of molecular phylogenies. This observation, while not proof positive that species selection is operating, does show that the raw material for species selection is present.

Species selection is no mere palaeontological oddity. It in fact seems to be both common and strong, although we do not know much about it yet. The fossil and molecular phylogenetic records can be used to measure the strength and direction of species selection. With that knowledge we can understand the types of traits and particular circumstances that promote or diminish diversification.

Summary

Diversification rates are not uniform across time, species or clades. When they vary systematically with one or more traits, it is known as species selection and may influence the change in frequencies of taxa or traits over time. Biologists working with either the fossil record or molecular systematics (using comparative methods) are interested in how diversification and traits covary to produce the biological patterns we observe today. Traits can cause diversification which can in turn influence the frequency of traits. Multiple traits can interact or influence diversification in complex ways. Price's theorem is a simple statement of how the change in the mean trait values over time is caused by selection along with any other evolutionary process and can be used to untangle selective differences in many traits and over time. The independent contribution of multiple traits to rate variation over time can be measured in both the fossil and molecular phylogenetic record. We demonstrate this approach using a time-calibrated phylogeny of labrid fish and show that sexual selection is a consistent cause of high diversification but morphological innovation is not. We also provide evidence that species selection is common in nature.

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