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SPECIES SELECTION AND THE MACROEVOLUTION OF CORAL COLONIALITY AND PHOTOSYMBIOSIS

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Differences in the relative diversification rates of species with variant traits are known as species selection. Species selection can produce a macroevolutionary change in the frequencies of traits by changing the relative number of species possessing each trait over time. But species selection is not the only process that can change the frequencies of traits, phyletic microevolution of traits within species and phylogenetic trait evolution among species, the tempo and mode of microevolution can also change trait frequencies. Species selection, phylogenetic, and phyletic processes can all contribute to large-scale trends, reinforcing or canceling each other out. Even more complex interactions among macroevolutionary processes are possible when multiple covarying traits are involved. Here I present a multilevel macroevolutionary framework that is useful for understanding how macroevolutionary processes interact. It is useful for empirical studies using fossils, molecular phylogenies, or both. I illustrate the framework with the macroevolution of coloniality and photosymbiosis in scleractinian corals using a time-calibrated molecular phylogeny. I find that standing phylogenetic variation in coloniality and photosymbiosis deflects the direction of macroevolution from the vector of species selection. Variation in these traits constrains species selection and results in a 200 million year macroevolutionary equilibrium.

KEY WORDS: **Diversification, multilevel selection, multivariate selection, paleobiology, phylogenetics.**

Species selection occurs when the processes of speciation and extinction act differentially on the properties of species. The net result of this selection is that the frequencies of species of particular phenotypes may change over time. Patterns in the fossil record are easiest to understand when you can go directly to an outcrop and observe and compare fossils in the rocks. Species selection cannot be understood in this way; it is a process that is too broad to observe in a single outcrop. By its nature, species selection involves many species over millions of years. The process of species selection itself is not directly preserved in the rocks, only its outcome, which sometimes take the form of large-scale trends.

Punctuated equilibrium (Eldredge and Gould 1972) plays an important role in the history of species selection because the patterns of punctuation and stasis are observable in the rock record. When combined with prior knowledge about large-scale trends, the occurrence of punctuated equilibrium implies another process that changes the average traits within a population of species even as each species itself remains static over its lifetime. Stanley (1975, 1979) fleshed out the hypothesis that this discrepancy between species with static traits and clade-level trends could be reconciled by species selection. The misfit between two patterns directly observable in the fossil record is explained by inferring the action of the big-picture process of species selection.

Inferring the action of species selection indirectly is less convincing than measuring its action directly. Indirect methods leave open the possibility that other processes could mimic species

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selection, which has spawned confusion and claims that species selection is not real (summarized by Grantham 1995). But even attempts at the direct measurement of the long-term action species selection in the fossil record can be equivocal (e.g., Lieberman et al. 1993) because the effects of other macroevolutionary processes are actually difficult to tease apart from species selection. The macroevolutionary changes caused by species selection are identical to the changes caused, for example, by phylogenetic evolution. Where species selection has successfully been identified directly is in the selective patterns of extinction during individual mass extinction events (e.g., Jablonski and Hunt 2006; Orzechowski et al. 2012). In these situations, phylogenetic changes cannot be confused for selection, because a comparison of victim and survivor species shows the direction action of species selection by extinction. They explicitly ignore the macroevolutionary changes that would be produced if the origination of recovery species were to be included by focusing their analysis on the comparison of victims and survivors. Mass extinction events, however, are rare events. Although the selectivity exhibited during these events shows that species selection is real, these selective events do not have the potential, in and of themselves, to generate sustained trends. For that, we have to look for species selection over long time series and try to partition the effects of species selection from other macroevolutionary processes.

Building on the work of Van Valen (1975), Arnold and Fistrup (1982b), and McShea (1994), I tried to measure the magnitude and direction of species selection and partition its effect on a trend in crinoids from phylogenetic changes in a temporally explicit way (Simpson 2010). Species selection is easily measured using the covariance between net diversification rates and trait values. I found evidence for a volatile temporal pattern of species selection, where at one time crinoids with simple skeletons diversify at higher rates than more complex crinoids, and other times the reverse was true. On average, species selection favored crinoids with simple skeletons and contributes to the overall trend toward simple skeletons. Measuring phylogenetic changes proved more difficult without a phylogeny. By using an indirect method based on McShea's (1994) "subclade test," which uses the relative skewness of total clade and subclade phenotypic frequency distribution to qualitatively estimate the magnitude and direction of phyletic and phylogenetic trends, I found evidence for a persistent tendency for crinoids with simple skeletons to evolve from crinoids with more complex skeletons. And so the trend toward crinoids with simple skeletons is caused both by species selection and by a tendency for simple crinoids to evolve from more complex ones. Far better than this indirect approach to phyletic and phylogenetic trends, a phylogenetic framework could be used to explicitly measure phenotypic changes in a clade. I was limited to only identifying a tendency of microevolutionary change, not measuring the actual amount of change.

Somewhat independently from the paleobiological approach to species selection, comparative phylogeneticists developed methods to measure diversification rates using time-calibrated molecular phylogenies (e.g., Nee et al. 1992a,b, 1994a,b; Nee and May 1997; Paradis 1997, 1998, 2004, 2007). Along with these methods for measuring diversification rates, Bokma and others (Bokma 2002, 2008; Mattila and Bokma 2008; Monroe and Bokma 2010; Ingram 2011) have developed explicit methods for measuring the exact phylogenetic changes that can produce trends.

Work has been progressing on methods to synthesize trait macroevolution and species selection (Maddison et al. 2007; Alfaro et al. 2009a,b; FitzJohn et al. 2009; Rabosky and McCune 2009; FitzJohn 2010, 2012; Rabosky 2012). The now standard methods, like BiSSE (Maddison et al. 2007) for binary traits and modifications for quantitative traits (FitzJohn 2010) implemented in the R package diversitree (FitzJohn 2012), the MEDUSA method (Alfaro et al. 2009b) in GEIGER (Harmon et al. 2008), and MECCA (Slater et al. 2012) offer powerful ways to tease apart species selection and trait evolution assuming that traits evolve according to one of a set of process models such as Brownian motion.

These methods offer powerful statistics for measuring macroevolutionary processes in relatively few parameters. They work best when the questions involve one trait and the average effect of species selection. When multiple traits interact, for example, dichromatism and jaw morphology in labrid fishes, it is difficult to tease apart the effects of each trait on diversification to identify which trait is driving diversification to what degree (Alfaro et al. 2009a). This is a problem of multivariate selection, where covarying traits interact and can produce complex responses to selection (Lande and Arnold 1983). The problem is amplified if selection and the covariance among traits both vary over time. In the labrid example, if the macroevolution of the two traits (dichromatism and jaw morphology) is treated in a temporally explicit and multivariate way, the answer becomes clear; dichromatism is always associated with high relative diversification rates while jaw morphology waxes and wanes in importance (Simpson and Müller 2012). The two traits in labrid fishes each evolve once in the phylogeny, so there was no need to use methods to measure the effects of trait evolution. However, traits may evolve in more complex ways, with increases or decreases in quantitative values or repeated gains and losses.

In this article, I present a complete approach to species selection and trait macroevolution that is based on Price's theorem. Trait macroevolution is treated as accumulated microevolutionary changes in a multilevel framework. I provide a general way to study macroevolution (even in the absence of a fossil record) in which species selection, cladogenetic change, and anagenesis can all interact and contribute to a resultant macroevolutionary

pattern. I illustrate this approach by focusing empirically on the macroevolution of photosymbiosis and coloniality in corals. These two traits in corals have been repeatedly gained and lost over their 250 million year history (Barbeitos et al. 2010), and are implicated in directly influencing diversification rates (Jackson and Coates 1986; Simpson and Kiessling 2010).

My Approach to Studying Multilevel Selection

Species selection operates on species in exactly the same way as natural selection does on organisms. Selection is the differential contribution of variant phenotypes to populations in the next interval of time, either in the next generation, or when members of current populations vary in age, some time in the future. The populations can consist of species or organisms, and the details of their respective life histories and mechanisms of inheritance do significantly affect the response to selection at each level. Despite these differences between levels in the mechanics of forming a descendant from an ancestor, the statistical differences between populations are what determine the response to selection and these statistical differences can be generalized to be formally the same across levels. Also, the organismal fitness components of birth and death have species-level homologues in speciation and extinction. But even at this higher level of focus, the generalized process of selection and how it affects the distributions of traits in the future is the same for organisms and species. These are formal similarities between selection at the organismal level and species selection.

I will use a generalized quantitative genetic model, Price's theorem (Price 1972), which is agnostic about a detailed mechanism of inheritance, and apply it to a multilevel macroevolutionary problem. This model forms the superstructure for my empirical macroevolutionary analyses, each specific empirical method serves to estimate a single parameter in this model. There are two ways to look at the utility of Price's theorem in this context. It serves as a guide for translating and comparing multiple analyses, unifying phylogenetic comparative methods with more paleobiological approaches. The mathematical details of Price's theorem also suggest specific aspects of the data to evaluate and I use it to untangle and partition the effects of species selection and phylogenetic change due to lower levels of selection.

Price's theorem (Price 1972) succinctly describes the changes a population's phenotypic distribution undergoes due to selection and other processes, and is easy to expand to consider multiple levels of selection (Hamilton 1975; Arnold and Fristrup 1982a; Rice 2004; Okasha 2007; Simpson 2010; Simpson and Müller 2012).

If we focus on how the population mean phenotype, $\bar{\phi}$, changes over time (the change in the population mean phenotype is denoted $\Delta\bar{\phi}$), we can identify the specific processes that act to change the mean phenotype. Price's theorem derives evolutionary processes algebraically from three well-established formal definitions of the statistics describing the frequency distributions of populations; the mean, the variance, and the covariance between two variables. In Price's theorem, the first key variable, ϕ, represents phenotypes, while the other variable, w, represents the fitness value associated with a particular phenotype. In its most basic form, the theorem separates the change in the mean phenotype of a population into the change due to selection and the changes of phenotypes in members of the population at different stages during their life cycles (Rice 2004; Frank 2012). The difference between the mean value of ϕ among member i's offspring and i's phenotype, is denoted $\bar{\delta}$. Price's theorem is

$$\Delta\bar{\phi} = \frac{1}{w}\left[\text{cover}(w, \phi) + E(\bar{\delta}w)\right]. \quad (1)$$

The magnitude and direction of selection is measured in the first covariance term. The second term, containing the expectation (denoted E(·)), measures the changes in phenotypes that accumulate from an ancestor to its direct descendants and any changes accruing during their lifetimes if they survive. In sum, the two main terms to come out of this equation is the selection differential, which measures the changes produced in the population due to species selection, and a term that estimates the directional change associated with anagenesis and cladogenesis.

Let us focus first on the selection differential, expanding the covariance term to identify any statistical signals that are easy to detect empirically. This is the change in the mean phenotype due only to directional species selection. We can understand the effects of species selection by temporarily ignoring any anagenetic or cladogenetic changes by setting $E(\bar{\delta} = 0)$ in equation 1. This highlights the selection differential, denoted S:

$$S = \frac{1}{\bar{w}}\text{cov}(w, \phi). \quad (2)$$

It will also be useful to unpack the covariance term of equation 2 into its component parts. Because covariances can be rewritten as $\text{cov}(x, y) = \beta_{y,x}\text{var}(x)$, we can express selection as a function of the linear regression of fitness on phenotype (Rice 2004):

$$S = \frac{1}{\bar{w}}\text{cov}(w, \phi) = \frac{1}{\bar{w}}\beta_{w,\phi}\text{var}(\phi). \quad (3)$$

This linear regression is a direct measurement of the magnitude and direction of species selection (Simpson 2010). Additional nonlinearities in the fitness-phenotype relationship could also result in stabilizing or disruptive selection and are independent of the directional component of selection measured by the linear regression. Lande and Arnold (1983; Rice 2004) found that

stabilizing selection can be measured by measuring the linear regression of fitness on the squared deviation of phenotypes from the mean phenotype; on a graph plotting phenotypes on the *x*-axis and fitness on the *y*-axis, a negative slope signifies stabilizing selection and a positive slope signifies disruptive selection.

The linear regression approach shown in equation 3 lends itself naturally to empirical application (Simpson 2010). The diversification rates of a set of species that share a common or a similar range of properties can be estimated directly from the fossil or molecular phylogenetic record with any of a number of common methods (Payne and Finnegan 2007; Simpson and Harnik 2009; Simpson 2010; Harnik et al. 2012; Simpson and Müller 2012). From the set of diversification rates and phenotypes, the linear regression representing species selection can be directly estimated. Of course, more complex models of fitness functions can be fit to the data (FitzJohn 2010), but the added complexity does little to increase the precision or accuracy of estimating directional selection over the linear regression approach, as a more complex fit estimates the joint effects of selection on multiple moments of the phenotypic frequency distribution.

Generally, the relevant measure of fitness (w) for species selection is the net diversification rate, which is the difference between speciation and extinction rates (Simpson 2010; Simpson and Müller 2012). This is because any change in the population of species is caused by traits values added by the origination of new species and traits lost by culling by extinction. The fitness of species is a mix of speciation and extinction, similar to the viability and fecundity components of fitness at the organismal level. All components of fitness contribute to the phenotypic changes in the population and only by combining their effects is the full effect of selection taken into account.

How is net diversification of species related to the familiar organismal-level fitness? One possibility is that diversification is a direct consequence of the evolution of organisms, or that fitness only manifests at the organismal level and percolates up to higher levels as a by-product (Vrba 1980; Charlesworth et al. 1982). Far from being a direct consequence, no relationship is necessary at all. Speciation and extinction are processes that are independent of the differential success of phenotypic variants within a species' constituent organismal populations. Otherwise speciation would be limited to the times when only the most fit phenotypes constitute a population, a condition unlikely to exist. Likewise, extinction occurs in every taxon independent of how much time the taxon has had to evolve (Van Valen 1973).

One consequence of organisms and species, both possessing fitness is that fitness itself has many levels. This is a view that is not commonly held even in explicit treatments in multilevel selection theory. In social evolution, it has long been assumed that group fitness must be the average of member fitness (Williams 1966). Species selection provides us with an opportunity to reevaluate this assumption, develop models where we can incorporate alternatives, and to study how fitness is hierarchically structured (Van Valen 2003; Simpson 2011).

Methods for Empirically Estimating the Terms in Price's Theorem Using Phylogenetic Data

Using time-calibrated molecular phylogenies of extant species provides an independent access to the macroevolutionary history of clades that even has some advantages over the fossil record. Phylogenetic information itself provides a direct measurement of cladogenetic evolutionary change (Bokma 2002; Ingram 2011). Suitably comprehensive phylogenies of fossil groups are rare, especially in species-rich clades of marine invertebrates. As a consequence, cladogenetic evolutionary trends have only been studied in small groups or by indirect phylogeny-free methods such as the subclade test (based on the skewness of the phenotype distributions of subclades McShea 1994; Simpson 2010). Within-species anagenetic change can only be observed in the fossil record with detailed stratigraphic sampling (Cheetham 1986; Roopnarine et al. 1999; Roopnarine 2001; Hannisdal 2006, 2007; Hunt 2007). But direct measurement of cladogenetic and anagenetic changes can be made with molecular phylogenies alone (Bokma 2002; Ingram 2011).

In molecular phylogenies, the summed length of branches that connect two species measure evolutionary divergence. These can be scaled to time by calibrating some nodes with the fossil record, and using a clock-like model of molecular divergence. The amount of phenotypic change over a single branch is a function of anagenesis and a contribution of unrecorded cladogenesis from extinct and unsampled extant species (Ingram 2011). Additional phenotypic changes can occur during speciation events due to cladogenesis. Species selection, cladogenesis, and anagenesis are all recorded in separate aspects of a time-calibrated phylogenetic tree with reconstructed ancestral states.

USING THE GEOLOGICAL TIME SCALE

Evolution plays out over time. Bokma's method for measuring cladogenesis and anagenesis (Bokma 2002; Ingram 2011) was designed to measure these changes summed over the whole tree from root to tips. A window of time is needed to tease apart anagenetic and cladogenetic changes, and for the Bokma method, this window of time encompasses the whole tree. Using the whole tree, the amount of evolutionary change due to anagenesis is the summed change from root to tip, which multiplies the summed branch lengths. Cladogenetic change is the phenotypic change from root to tip times the number of nodes. To capture the dynamics (and their variation), I perform my analyses repeatedly

in stage-level intervals of geological time. The main advantage to using a discrete time scale is that it allows the measurement of component processes without an explicit model easier. Just as in estimating integrals in calculus, the flaws of many small estimates can cancel out yielding a better understanding than only few flawed estimates would provide. An added bonus is that these results can be directly compared to other patterns in the geological and fossil record because this time scale is the same used to describe patterns in the fossil and geological record.

PARTITIONING MACROEVOLUTIONARY PROCESSES IN A PHYLOGENETIC FRAMEWORK

I track the evolution of two traits simultaneously using a simplified and multivariate matrix form of Price's theorem (Rice 2004):

$$\Delta\bar{\phi} = \mathbf{CP}^{-1}\beta_{w,\phi} + \bar{\delta}. \quad (4)$$

The degree to which there is a trend in the traits is measured by $\Delta\bar{\phi}$. The "heritability" of traits, the similarity between ancestors and descendants in their traits, is given by the matrix C, and the P^{-1} is the variation and covariation among traits among species. Species selection is measured in $\vec{\beta}_{w,\phi|}$. And $\bar{\delta}$ takes into account the changes in trait values due to anagenesis within species and cladogenesis among species.

The diversification and trait variables (w *and* ϕ) are vectors with elements for each trait of interest. P^{-1} is equal to the inverse of the phenotypic variance–covariance matrix:

$$\mathrm{P} = \begin{bmatrix} \mathrm{var}(\phi_1) & \mathrm{cov}(\phi_1, \phi_2) \\ \mathrm{cov}(\phi_2, \phi_1) & \mathrm{var}(\phi_2) \end{bmatrix}$$

and C is the ancestor-descendant covariance matrix:

$$\mathbf{C} = \begin{bmatrix} \mathrm{cov}(\phi_1^o, \phi_1) & \mathrm{cov}(\phi_1^o, \phi_2) \\ \mathrm{cov}(\phi_2^o, \phi_1) & \mathrm{cov}(\phi_2^o, \phi_2) \end{bmatrix},$$

where ϕ_1^o is the mean phenotype of descendant species with trait i. The C matrix is constructed by measuring the covariance between ancestor and descendant species for combinations of all traits. For two traits, that means four covariances are calculated: the covariance between ancestor and descendant species in trait 1, the covariance between ancestors with trait 1 and descendants with trait 2, the covariance between ancestors with trait 2 and descendants with trait 1, and the covariance between ancestor and descendant species with trait 2. The C matrix is constructed from the same information that is used to measure $\bar{\delta}$, but summarizes this information a different way. This matrix takes this information and converts it to a form that describes the deviation from the selection vector the population will take given the cladogenetic and anagenetic changes that occur.

In equation 4, $\bar{\delta}$ is a vector, with elements describing the change mean value (or relative frequency) of each trait due to anagenesis and cladogenesis. If, for example, traits are evolving by Brownian motion, there will be changes among individual ancestor-descendent lineages, but the change on average, across lineages will be equal to zero.

I directly measure each of these terms in the macroevolutionary molecular record. Because there are no known unknowns, each term can be directly measured in a phylogeny, the equality should be closely met. The change in phenotypes should be accounted for by the sum of the change due to species selection, the phenotypic and ancestor-descendant covariance matrices, and the vector of phylogenetic changes.

The left-hand term, $\Delta\bar{\phi}$, estimates the observed change in the mean population phenotype over time and is measured as the relative frequency of binary traits or the inferred mean phenotype. This term describes the degree to which there is a trend in the traits.

The phenotypic covariance matrix P is measured directly from the nodes and lineages present in each time interval, and the ancestor-descendant covariance matrix C is measured directly from the phylogenetic relationships between lineages present in time t and their descendants in time $t+1$.

The estimates of the magnitude and direction of species selection is given by the vector $\vec{\beta}_{w,\phi|}$. In a univariate situation, selection can be measured by the linear regression. But in the present multivariate situation, the independent selection coefficients are best estimated using multiple regression (Lande and Arnold 1983; Rice 2004). Each element in $\vec{\beta}_{w,\phi|}$ is a partial regression coefficient derived from a multiple regression analysis. Time series of diversification rates are calculated using the method for sets of lineages and nodes that have similar phenotypes using the method of Simpson et al. (2011, 2012). If a trait drives diversification, it should show a consistent association with diversification rates. Hitchhiking traits, or traits that are associated only indirectly with diversification may show a more variable association with diversification (Simpson and Müller 2012). In each interval, diversification rates (w) are a function of the number of nodes and the sum of all branch lengths in the interval, including those that do not speciate. The time span represented by a geological stage is Δt_s, and the youngest age of the stage is t_s. If the number of nodes in a stage is denoted k_s and the number of separate lineages entering the stage is equal to n, and assuming that diversification rates follow a truncated exponential distribution (Nee et al. 1992b; Nee 2001), then the maximum-likelihood estimate of the diversification rate is equal to:

$$\omega = k_s / \left[(n - k_s)\Delta t_s + \sum_{i=1}^{k_s} (t_i - t_s) \right]. \quad (5)$$

The denominator has two terms corresponding to lineages ranging through the time interval without branching and lineages branching inside the interval. The summation measures the total length of branches for lineages arising in the window of observation. The product $(n - k_s)\Delta t_s$ measures the total length of lineages that range though the interval without branching.

I modified Bokma's method (Bokma 2002; Ingram 2011) for partitioning phenotypic changes that accumulate anagenetically and cladogenetically along phylogenies. For my derivation here I assume continuous traits for generality, then modify the equations for the binary traits I use in the analysis.

Anagenetic change accumulates within species over time and cladogenetic changes occur during speciation. In a phylogenetic context, the amount of anagenesis is a function of the lengths of branches whereas cladogenesis is a function of the number of speciations. Bokma's method (Bokma 2002, 2008; Mattila and Bokma 2008; Monroe and Bokma 2010; Ingram 2011) estimates the total change in the phylogeny and partitions it into a single estimate that sums the anagenetic and cladogenetic components. Both the magnitude and direction of phenotypic change is captured in the raw difference in phenotypes between descendants and ancestors, $\phi' - \phi$.

Phenotypic change due to anagenesis along a single branch is the amount and direction of change multiplied by the amount of time elapsed, or $(\phi' - \phi)\Delta t$. Similarly, cladogenetic change along a single branch is the amount of change from one stage to the next multiplied by the number of cladogenetic events (k), or $(\phi' - \phi)k$. And the total phenotypic change along a single branch is the sum of anagenetic and cladogenetic change, $(\phi' - \phi)\Delta t + (\phi' - \phi)k$.

I want to know the average phenotypic change across all branches from stage to stage. Because cladogenesis increases the number of lineages over time, N is equal to the number of lineages present at the end of a time window. For a single continuous trait, the average phenotypic change, $\bar{\delta}$, is equal to:

$$\bar{\delta} = \frac{1}{N}\sum_{i=1}^{N}[(\phi - \phi)\Delta t + (\phi - \phi)k]. \quad (6)$$

Equation 6 shows the general form of the amount of phylogenetic change for a continuous trait. For binary traits, which do not have intermediary states along branches, the anagenetic term of equation 6 must be modified slightly. The change in the mean phenotype, calculated for continuous traits needs to be replaced by the change in relative frequency. I want the average of the sum of the phenotypic changes in a time window along each branch:

$$\bar{\delta} = \frac{1}{N}\sum_{i=1}^{N}(\phi - \phi). \quad (7)$$

When traits are binary, we track the changes in relative frequency by summing the changes along each branch during a window of time. State changes 0 to 1 equal 1, whereas changes from 1 to 0 equal −1. No changes (0 to 0 or 1 to 1) equal 0. Figure 1 provides an example of all possible changes, including no changes due to range through lineages. In this example, no net change in frequency occurs despite a number of state transitions. Importantly, in binary characters, it is not possible to distinguish between anagenesis and cladogenesis like it is using equation 6 for continuous traits unless state changes can be dated to occur along a branch rather than at nodes (Goldberg and Igić 2012; Magnuson-Ford and Otto 2012).

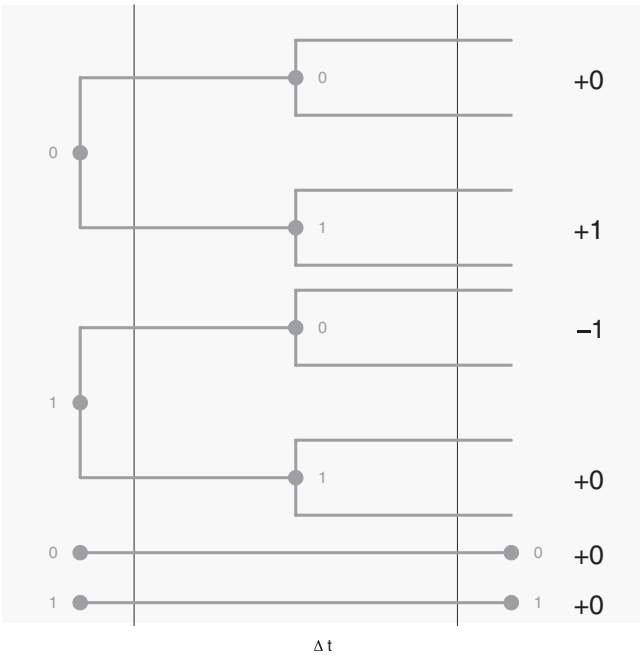

Figure 1. An illustration of how to tally the change in frequency due to phylogenetic evolution of a binary trait. When the frequency of character state 1 is tracked, the difference between descendants and ancestors measures its change over time. Transitions from state 0 to 0 gives no change. Transitions from 1 to 1 also gives no change. Transitions from 1 to 0 change the frequency by −1, and similarly a change from 0 to 1 changes the frequency by +1.

Species selection and phylogenetic changes are integrated by substituting equation 6 or 7 into equation 4 to give:

$$\Delta\bar{\phi} = C P^{-1}\beta_{w,\phi|} + \frac{1}{N}\sum_{i=1}^{N}[(\phi, \phi)\Delta t + (\phi, \phi)\kappa] \quad (8)$$

for continuous traits and

$$\Delta\bar{\phi} = \mathbf{C}\mathbf{P}^{-1}\beta_{w,\phi|} + \frac{1}{N}\sum_{i=1}^{N}(\phi - \phi) \quad (9)$$

for binary traits.

All of these equations are easily modified to work with continuous or discrete characters as needed by converting between

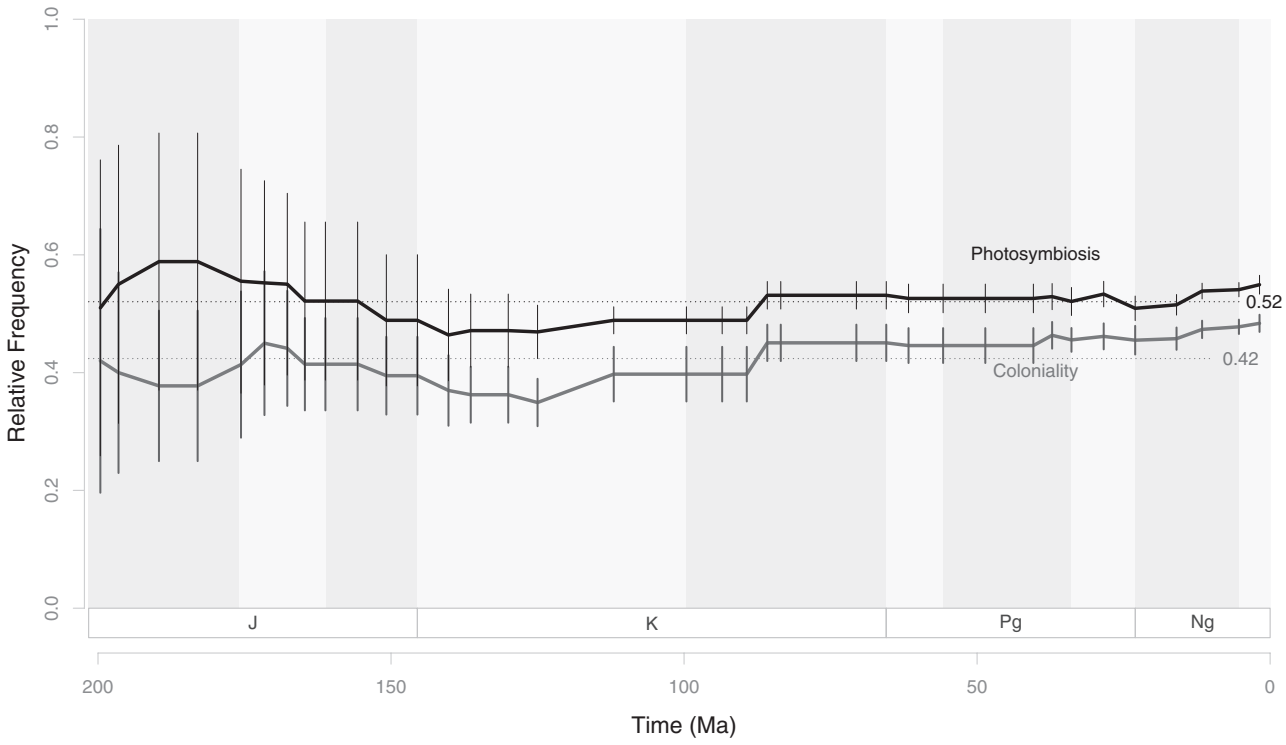

Figure 2. **The relative frequency of photosymbiosis and coloniality in scleractinian corals over the last 200 million years. The long-term average relative frequency for each trait is plotted. J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene.**

mean phenotypes and the relative frequency of phenotypes. These equations work as well with fossil data as they do for molecular phylogenies. Most importantly, linear regression estimates of species selection made from discrete and continuous traits and from molecular phylogenetic and fossil records are all directly comparable to each other (Simpson and Müller 2012) despite the inherent bias in raw estimates of diversification rates from molecular phylogenies (Simpson et al. 2011) as long as species selection is measured as differential net diversification.

Estimating each term empirically requires a prior reconstruction of ancestral states. Reconstructions of ancestral states are the weak link in all macroevolutionary analyses of phenotypic macroevolution. Currently, the best methods, BiSSE and relatives, control for species selection in their reconstructions (FitzJohn et al. 2009; FitzJohn 2010, 2012).

Photosymbiosis and Coloniality in Scleractinian Corals

Only half of extant coral species have symbionts (Veron 2000). This makes corals exceptional among symbiotic clades because symbiosis is more commonly an all or none phenomenon. For example, most vascular plant species have symbiotic mycorrhizal fungi associated with their roots. Near the other extreme, out of the thousands of bivalves, photosymbiosis is found only the eight modern species of Tridacnid clams (including the giant clam *Tridacna*).

Photosymbiosis in corals is ancient (Stolarski et al. 2011). It most likely evolved in the Triassic, fairly early in the evolution of scleractinian corals (Stanley and Swart 1995; Stanley 2003; Barbeitos et al. 2010). This long history of photosymbiosis suggests that it is unlikely that we just happened to live in the time when corals are the act of becoming predominately photosymbiotic. Rather, because of the early origin and long history of photosymbiosis, it seems more likely that the relative frequency of photosymbiosis today is the result of one or a few long-acting processes. Some processes must be keeping photosymbiosis around but preventing it from becoming ubiquitous. What is the source of this potential equilibrium between photosymbiotic and nonphotosymbiotic scleractinians?

Today and in the past, coral photosymbiosis is closely associated with coloniality (Barbeitos et al. 2010). The extra energy that the photosymbiotic zooxanthellate algae produces is channeled by the coral into colonial growth (Coates and Jackson 1987). The metabolic by-products of photosymbiosis also boost the rate of precipitation of the coral's skeletons (Davies 1984) and allows for a greater size and higher integration of the coralites (Coates and Oliver 1973; Jackson and Coates 1986; Coates and Jackson 1987). In return, this increased growth of colonial corals can keep the zooxanthellae bathed in sunlight because these

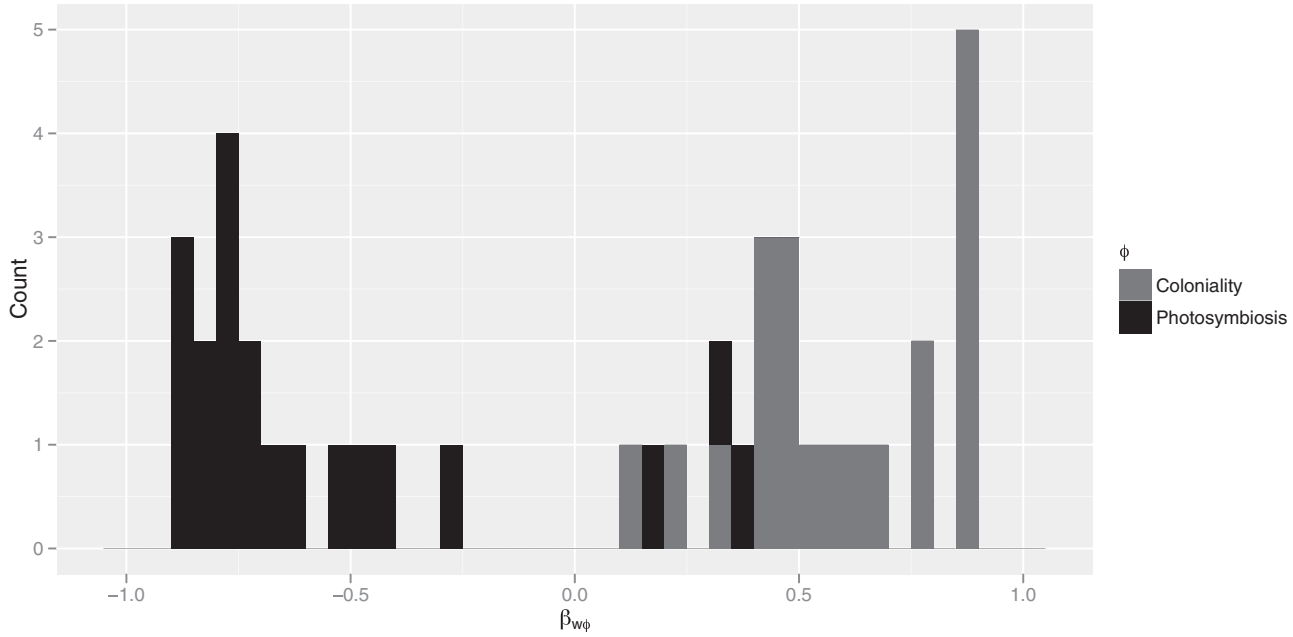

Figure 3. **A histogram of selection vectors for coloniality and photosymbiosis. $\beta_{w,\phi}$ is the magnitude and direction of selection for each trait, independent of the other trait. The counts represent the number of time intervals that selection is of a particular magnitude. Positive values mean that selection is for the trait (either coloniality or photosymbiosis). Negative values are against that trait (for solitary or nonphotosymbiotic corals). These histograms are stacked, so the bars at 0.27 show the counts of coloniality and photosymbiosis plotted on top of each other. Each trait has only one interval at that magnitude and direction.**

corals can grow clonally up out of the shade produced by other organisms. Covariation among traits, as coloniality and photosymbiosis exhibit, can influence the way that each trait evolves. Lande and Arnold (1983) provide the theory of multivariate natural selection that is epitomized by the evolution of coloniality and photosymbiosis. Coloniality covaries with photosymbiosis, and in this multivariate situation, macroevolution by organismal advantage balanced by species extinction in either coloniality (Jackson and Coates 1986) or photosymbiosis (Kiessling 2009) is unlikely. The evolution of multiple correlated characters follows a more complex path than expected by considering any single trait in isolation.

There is one major hurdle to overcome in studying the macroevolution of coral photosymbiosis in the fossil record. Photosymbiotic corals are limited to warm shallow seas (Veron 2000). In contrast, nonphotosymbiotic corals, while not limited to warm shallow seas are common in the deep-water cold oceans (Cairns 2007; Roberts et al. 2009). Unfortunately, the fossil record of deep-water corals is not as well understood as the shallow-water fossil record or zooxanthellate corals. This discrepancy in the quality of the fossil record therefore impedes our ability to study the macroevolution of photosymbiosis directly. To circumvent this problem I use time-calibrated molecular phylogenies of extant coral species as the raw data in this analysis.

TIME-CALIBRATED MOLECULAR PHYLOGENY

For this analysis, I use a well-resolved comprehensive molecular phylogeny of scleractinian corals (Kitahara et al. 2010). This tree consists of approximately 240 species drawn from all groups of scleractinians. Time calibration was done using a maximum-likelihood estimate of the mean path length (Sanderson 1997) with the base of Scleractinia dated to 254 million years ago (Mya) following Simpson et al. (2011). Although this tree represents under 20% of the near 1300 extant species, previous work on coral phylogenetics and diversification (Simpson et al. 2011) suggests that due to pulsed diversification rates, even a relatively undersampled tree provides robust estimates of the pattern of diversification rates. Because species selection measures the relative difference in diversification rates, any distortion in the absolute magnitude of the rates will not affect the results. Likewise, cladogenetic changes from missing or unsampled species contributes to the change due to anagenesis, missing species still contribute to the overall phylogenetic changes (Ingram 2011; Rabosky 2012). Because I am interested in the total change, the sum of anagenetic and cladogenetic change, in this analysis, the effects of missing lineage will be minimized. I reconstructed ancestral states for coloniality and photosymbiosis using a discrete maximum-likelihood model where gains and losses of states are both possible. Ancestral state reconstruction was done in R using the ace function in the ape package using an all rate different model (Paradis et al. 2004) and

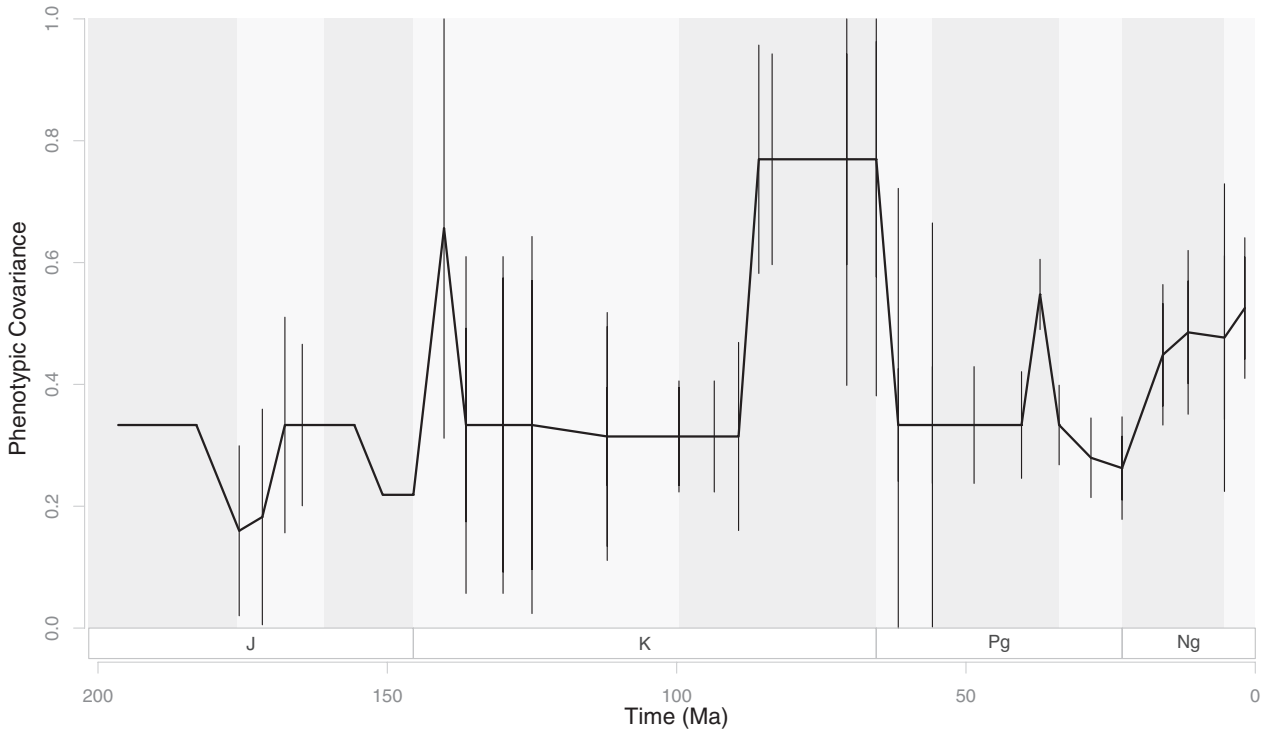

Figure 4. **The temporal pattern of the phenotypic covariance between coloniality and photosymbiosis. The value plotted is the symmetric off-diagonal value of the matrix P. J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene.**

the presented results are averaged over states with plus or minus two units of log-likelihood.

GEOLOGICAL TIME SCALE

I measure the total change in frequency of coloniality and photosymbiosis, species selection, and phylogenetic changes within geological stages. Because scleractinians experienced a major mass extinction at the end of the Triassic (Kiessling and Aberhan 2007; Kiessling 2009; Simpson and Kiessling 2010) there is a distinctive gap of nodes in the molecular phylogeny (Simpson et al. 2011). To avoid this discontinuity I begin my analysis in the Jurassic at 201.6 Mya. I use the stage-level time scale defined by Gradstein et al. (2004) resulting in 36 intervals of time with an average width of 5.6 million years.

Results

In scleractinian corals, the relative frequency of photosymbiosis and coloniality has both been approximately constant over the last 200 million years (Fig. 2). Photosymbiosis is the more common strategy, comprising 52% of species on average since the Jurassic. On average, 42% of species are colonial.

Species selection ($\vec{\beta}_{w,\phi|}$) for coloniality has varied in magnitude, but maintains a constant direction until the Neogene, 23 Mya. Colonial species have a consistently higher diversification rate than solitary species. Remarkably, selection is consistently against photosymbiosis; photosymbiotic species diversify at relatively lower rates than nonphotosymbiotic ones (Fig. 3).

Together, P and C control the response to selection. The P matrix, showing the covariance between photosymbiosis and coloniality in contemporary species is always positive (Fig. 4). When phylogenetic changes do occur, they tend not to break this covariation. Of the approximately 50 character state transitions, only 15 break the covariation, or about 30%, but these always co-occur in time with transitions that reinforce the covariation. The ancestor-descendant covariance matrix (C) always has nonzero values in the off-diagonal (Fig. 5) which translates into a direction of evolution that does not coincide with the direction of the selective vector.

The average magnitude of phylogenetic changes ($\bar{\delta}$) in relative frequency is 0.01 for coloniality and 0.003 for photosymbiosis (Fig. 6). But most time intervals show no directional change in frequency due to phylogenetic evolution. The median change for both traits is equal to 0.

Because the median value of $\bar{\delta}$ for both traits is zero, selection ($\vec{\beta}_{w,\phi|}$) and the response to selection determined by P and C determine the overall change in frequency of coloniality and photosymbiosis ($\Delta\bar{\phi}$). This occurs because the phenotypic and ancestor-descendent covariance matrices divert phenotypic changes from the maximum gradient vector of species selection. The resulting selection differentials (S) are near zero (Fig. 7).

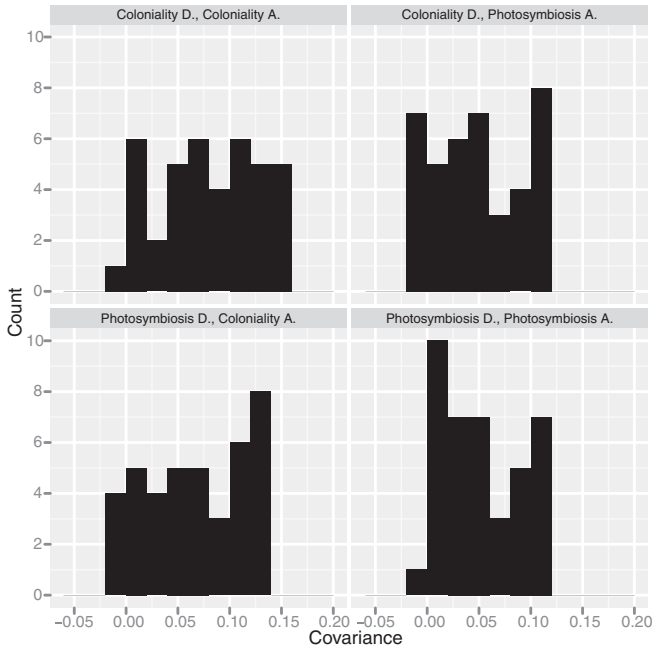

Figure 5. Histograms showing structure of the ancestor-descendant covariance matrix C. Each histogram is one element of the matrix. Counts represents the number of time intervals in which element has a particular covariance. D, descendants; A, ancestors. The off-diagonal elements of C are never equal to zero.

Discussion

Despite a strong vector of species selection for nonphotosymbiotic colonial corals, there is no response to this selection due to the structure and phylogenetic evolution of variation measured by P and C. Photosymbiosis and coloniality remain tightly integrated in coral species, and as a consequence an equilibrium frequency of coloniality and photosymbiosis is maintained over geological time by the balance between species selection and the limited and orthogonal production of variation across the phylogeny. Microevolution is constraining species selection in a way analogous to a microevolutionary situation where genetic constraints impede adaptive evolution (e.g., Conner and Via 1992). In a macroevolutionary system, the variation that species selection acts on arises from microevolutionary processes.

In corals, colonial growth at the level of individual colonies is aided by increased calcification rates and excess energy by the coral's photosymbiosis with *Symbiodinium* (Muscatine 1990). A photosymbiotic relationship is inferred to be present early during the geological history of scleractinian corals (Stanley and Swart 1995). This phylogenetic analysis and the one by Barbeitos et al. (2010) both support the early evolution of a coupling between coloniality and photosymbiosis that is maintained over at least 200 million years (Fig. 4). It is reasonable to infer that the

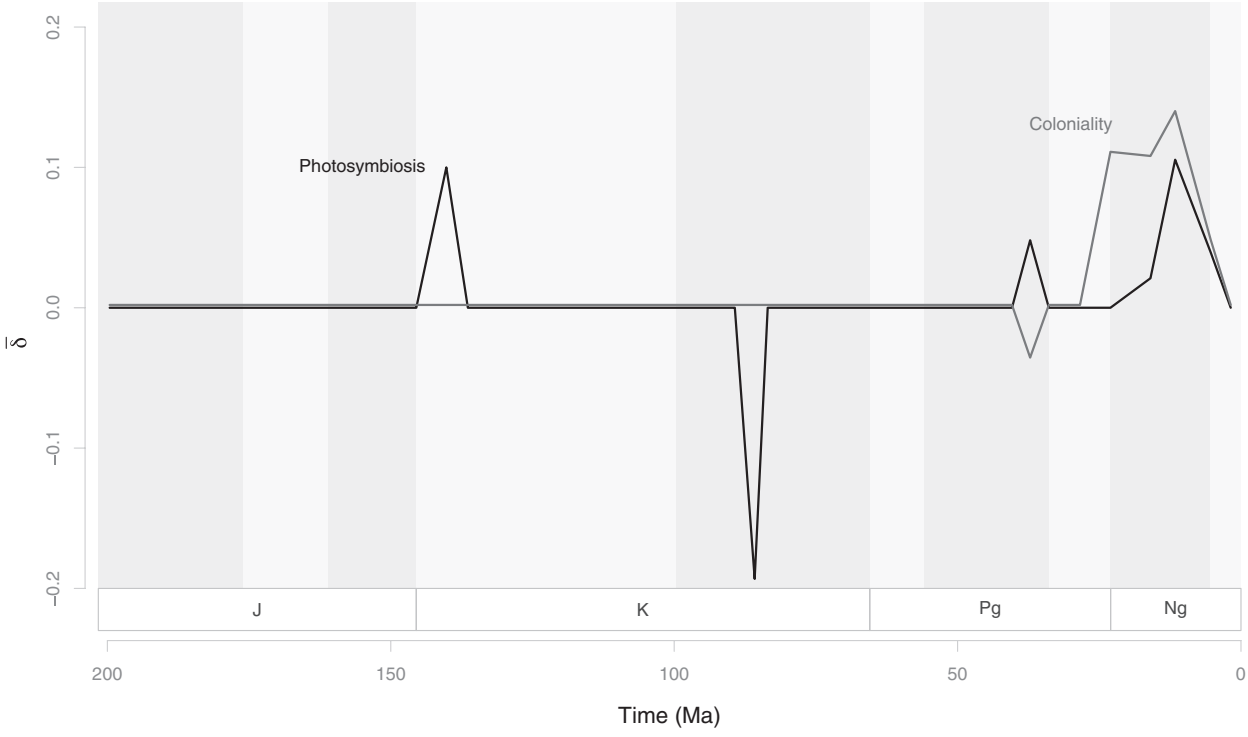

Figure 6. The temporal pattern of phylogenetic change in relative frequency for coloniality and photosymbiosis. J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene.

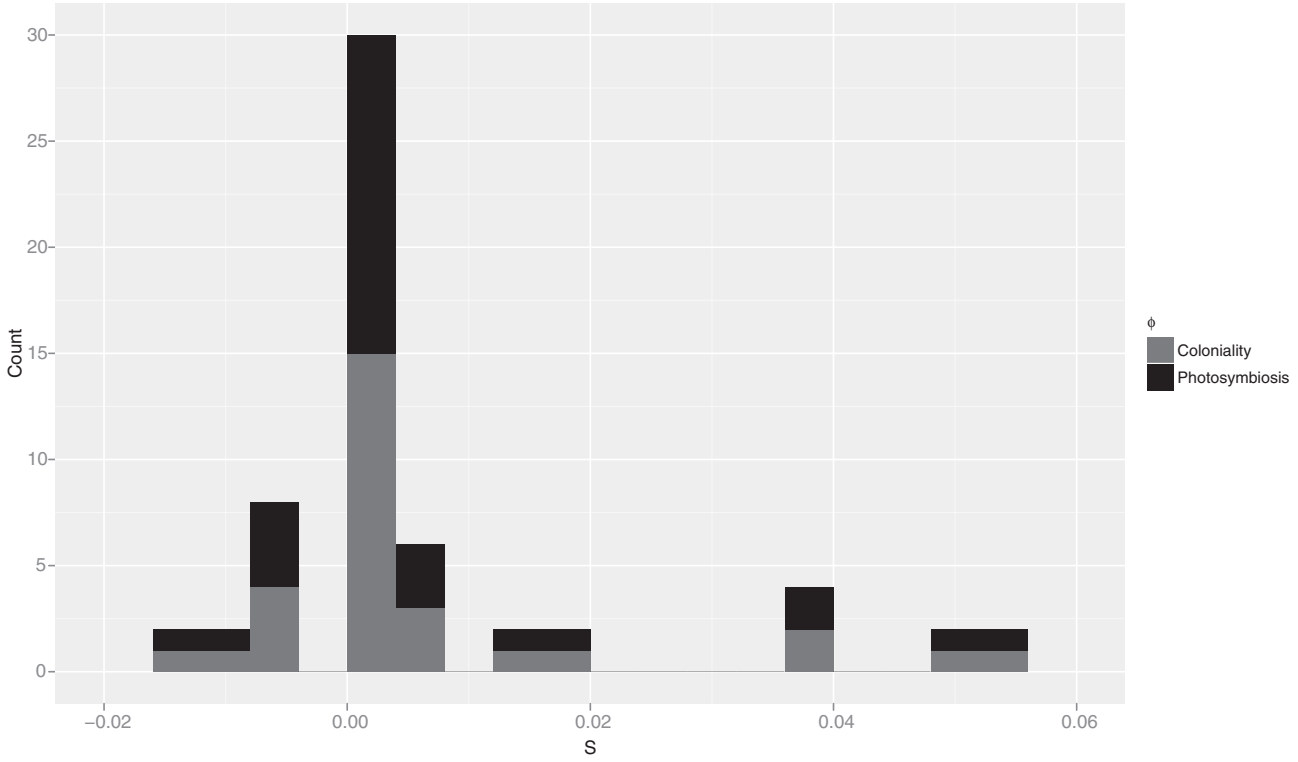

Figure 7. Histogram of the observed change in relative frequency response to the species selection differential (S), which is the product of the selection vector, the phenotypic covariance matrix, and the ancestor-descendant covariance matrix. Counts show the number of geological stages with a particular response to selection.

long-term link between coloniality and photosymbiosis has been due to the physiological and growth advantage that photosymbiotic colonies have (Coates and Jackson 1987) because only about one-third of state transitions break the coupling between these traits. Enough variation among species is produced for selection differentials to be measured, but not enough to change the response to selection. The ancestor-descendant covariance matrix is consistently nonzero in the off-diagonal elements, deflecting and dampening the selection vector.

Selection among multiple traits provides many more opportunities for selection at high levels to be important. For most of the post-Triassic history of corals, species selection favored nonphotosymbiotic colonial species, but there was no response to this selection due to limited production of variation. The resulting equilibrium is due to the action of both levels of selection and multiple traits. Without the joint action of both levels, this equilibrium would not occur.

IMPLICATIONS

Gould (2002) believed that phenotypic stasis and cladogenesis with random direction would maximize the ability for species selection to cause macroevolutionary change. When his conditions are met, no microevolutionary selective vector is possible and random directional cladogenesis would still produce sufficient variation for species selection to act. The coral example and the macroevolutionary application of Price's theorem presented here shows that Gould's thinking is wrong. Especially with multiple covarying traits, anagenesis, cladogenesis, and species selection can interact in complex ways.

From the view of macroevolution in equation 4, the direct evolutionary change attributable to cladogenesis and anagenesis is concentrated in the single term $\overline{\delta}$. The effects of anagenesis and cladogenesis can be partitioned (eqs. 6 and 7, but partitioning them has no bearing on the strength of species selection, which is wholly independent from the tempo and mode of phenotypic change. Similarly, both anagenesis and cladogenesis both contribute to the structure of the ancestor-descendant covariance matrix, C, and so they influence how the macroevolutionary response to selection. The structure of the C matrix may augment the response to selection or hinder it, and the relative contribution of anagenesis and cladogenesis to C may or may not predict the response to selection.

The structure of the C matrix is determined exclusively by the patterns produced by microevolutionary processes and the C matrix determines the response to species selection. Clearly, in order for species selection to act it requires the variation that microevolution produces to be structured in a concordant way. Although the importance of the C matrix (or when the narrow

sense of heritability is used, the **G** matrix) is obvious in quantitative genetics, paleontologists have rarely recognized the importance of high-level heritability (except, e.g., Jablonski 1987; Rice 1995). In much the same way as natural selection is not possible without mutation, macroevolution would not be possible without microevolution.

Rabosky (Rabosky and McCune 2009, 2012) points out that models of trait evolution tend to ignore species selection to their detriment. Process models of phenotypic evolution on a phylogeny, such as Brownian motion or the Ornstein–Uhlenbeck (O-U) process ignore the action of species selection. The equilibrium frequency of coloniality and photosymbiosis produced by the interaction of species selection and phylogenetic trait evolution superficially resembles the results of an O-U model where clades evolve toward an optimal phenotype and remain near it. The interplay between species selection and microevolution may produce this equilibrium without the need for an optimal phenotype. If so, empirical studies that find support of O-U may be caused by species selection.

When the Price formulation is made, it is easy to see how limited a strict single-level macroevolutionary explanation is. If macroevolution patterns are only caused by microevolution processes, there is no extinction, speciation, or diversification selectivity, and phylogeny is less important than the changes that accumulate within species. A similar statement is true for every other multilevel situation in biology. A fully reductionist selective scenario makes a strong prediction about how higher level emergent fitnesses should correlate with phenotypes: that is to say no correlation at all, ever. This could be true in principle, but in fact nonzero values are commonly observed in nature. Some multilevel regime must be at work.

Species selection is an important end-member scenario in multilevel selection. Speciation and extinction are clearly independent of organismal birth and death and consequently the demographic aspects of selection at each level are easily and clearly identified. This independence provides an ideal opportunity to derive expectations of how levels interact with each other. The lessons learned from the study of species selection are relevant to the general discussion of multilevel selection. Because of the emergent nature of extinction and speciation, there is no need to worry about bookkeeping; tracking the constituents of species is unnecessary to measures of species selection. In other multilevel systems, the distinction between groups, colonies, and societies and their constituents is rarely as clear-cut as it is between species and their members. Species selection provides us with an opportunity to understand the full structure of multilevel selection in its most emergent form.

Lessons from species selection can lead to new questions about how multilevel selection works in other systems. For example, it has been historically assumed that group-level fitness is equal to the mean member-level fitness. The mean fitness of members is always equal to the growth rate of that population and the assumption is that this growth rate somehow translates into the birth and death of whole groups. The independence between fitness at the organismal and species levels illustrates how peculiar this assumption is. Speciation and extinction are not considered to be equivalent to the population growth rate of their constituent organisms. In other multilevel systems, such as social insects, human groups, or colonial invertebrates, is there any aspect of the demographics of those groups that is, like speciation, independent of the growth rate of their populations? My feeling is that the answer to this question would go a long way to understanding multilevel selection and the transitions in individuality (Simpson 2011, 2012).

However, the population growth rate is an important parameter and may be crucial in the initial emergence of new levels of selection (Simpson 2011). Initially, emergent levels may not have a mechanism of reproduction. The only component of fitness they possess is similar to growth. To highlight the evolutionary importance of growth, Van Valen termed this component of fitness "expansion" (Van Valen 1976, 1989). Expansion has rarely been empirically explored in any multilevel situation. In macroevolution, expansion of species may be expressed in their spread across the globe or in changes in their abundances. Species do tend to show a tendency to start small and expand to a maximum occupancy near the middle of their lifetimes then decline toward extinction (Foote 2007; Foote et al. 2007; Liow and Stenseth 2007; Liow et al. 2010). Is this pattern an example of macroevolutionary expansion? Expansion could also be critical to the transitions in individuality (Simpson 2011) as it potentially explains why colonies with a life-history emphasizing growth (like corals) remain morphologically simple for hundreds of millions of years, whereas colonies with a life history emphasizing colony reproduction (such as some bryozoans) evolve a high degree of within-colony polymorphism easily (Simpson 2012).

EMPIRICAL SUMMARY

Colonial but nonphotosymbiotic coral species tend to have the highest relative diversification rates. Yet, corals of this type are not the most common today. Coral species tend to be either colonial and photosymbiotic or solitary and nonphotosymbiotic. This variation deflects the direction of macroevolution from the vector of species selection. In other words, despite strong and consistent species selection, the variation available does not allow a response to species selection. A summary illustration of the interaction between selection and variation is shown in Figure 8. This interaction between selection in one direction and variation in another results in an equilibrium frequency of coloniality and photosymbiosis that is maintained fairly consistently since the Jurassic, 200 Mya.

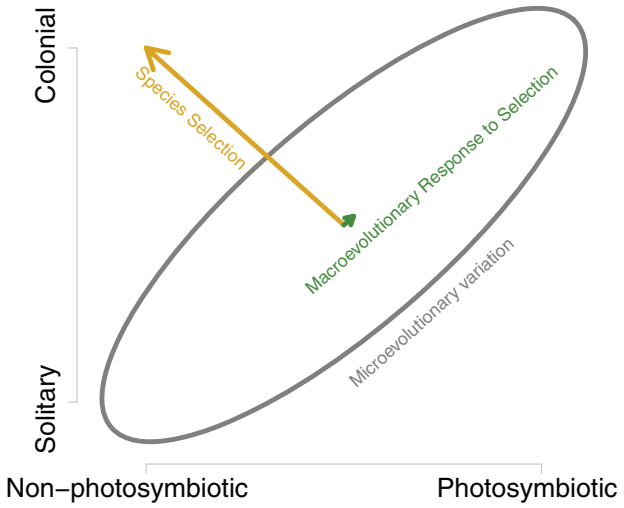

Figure 8. **Summary illustration showing the macroevolutionary response to direction of species selection relative to the standing variation in coloniality and photosymbiosis. The species selection vector points toward colonial but nonphotosymbiotic species, which have the highest relative diversification rates. The ellipse represents the standing variation of coloniality and photosymbiosis among species. The majority of species are colonial and photosymbiotic or solitary and nonsymbiotic. The resultant vector of macroevolutionary change is a product of species selection and the variation among species. Microevolutionary variation constrains the macroevolutionary response to species selection.**

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