A Genetical Theory of Species Selection

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Species selection, differential rates of speciation or extinction resulting from species level characters, is often invoked as the main mechanism of macroevolution that is not simply an extension of microevolutionary processes. So long as we are careful in defining "species", the logic of species selection is sound. This does not mean, however, that this process can influence evolutionary dynamics under realistic conditions. The principal challenge to the efficacy of species selection as an evolutionary mechanism is the idea that selection between individuals within species will be so much more efficient as to swamp out any effects of selection between species. To assess this, a genetic model is constructed that includes simultaneous selection within and between species, and this is used to ask: under what conditions could species selection influence evolutionary dynamics, even in the face of opposing selection between individuals? The model shows that the efficacy of species selection is strongly determined by the time between speciation events (measured in individual generations), the mutation rate of the character under consideration, and the initial size of a newly formed reproductively isolated population. Data indicate that a few studied lineages have shown sufficiently high speciation rates to make species selection an important mechanism in the evolution of characters with mutation rates on the order of 10^{-6} per generation. Quantitative characters, such as body size, generally change too readily for species selection to be relevant to their evolution. Complex characters, however, may be good candidates to be influenced by species selection. The interaction of selection within and between species can be subtle, with individual selection looking, from the standpoint of a species, very much like development of an individual. Furthermore, selection between individuals may be the main process assembling complex adaptations, while species selection allows them to persist over long periods of time.

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Introduction

A species, like an individual organism, can possess characters that influence its chances of surviving or of producing a descendant. If we define "species" as a population that remains reproductively isolated from others for a long time, then such species level characters include geographic range and allele frequency. If these characters vary between different species, then such species have what it takes to be units of selection. This has led a number of authors to argue that selection between species may be an important

evolutionary mechanism. In particular, species selection has been invoked as a factor in the evolution of body size and geographic range (Levinton, 1988), dispersal patterns (Jablonski & Lutz, 1983), the prevalence of sexual reproduction (Stanley, 1979), extinction resistance among clades (Jablonski, 1987), and patterns of species abundance (Gilinsky, 1987). The fact that different parts of a clade often show more variation in branching rates than would be expected by chance (Guyer & Slowinski, 1991; Kirkpatrick & Slatkin, 1993) points to the potential for selection between lineages, and the demonstration that characters associated with species level fitness are heritable across speciation events (Jablonski, 1987)

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points to the potential for this selection to influence evolutionary dynamics.

The degree to which this potential is realized, however, depends on the amount of heritable variation between species (Slatkin, 1981), which is itself strongly influenced by selection between individuals. Not only can individual level selection eat up variation between related species, the heritability of a species level character (such as an allele frequency) is reduced if selection between individuals changes that character between formation of a new species and the time that it first spins off a daughter species. The most potent challenge to the efficacy of species selection has thus been the argument that because the generation times of individuals are (by definition) much shorter than the lifespan of a species, selection between individuals will swamp out any effects of selection between species. Any general model of species selection must therefore include the effects of selection between individuals. I present such a model below, and use it to investigate the conditions under which species selection could influence evolutionary dynamics, even in the face of opposing selection between individuals.

Most models of group selection follow the standard approach in population genetics of tracking the frequency of alleles (calculated across many groups) over time. This works so long as the frequency of different types of groups (i.e. groups with different compositions) can be reconstructed from overall allele frequencies. To ensure that this last condition is met, most models have groups reproducing by contributing individuals to a "migrant pool", out of which new groups form (Levene, 1953). In such a case, if new groups form as random samples of individuals from the migrant pool, we can construct a generalized "Hardy–Weinberg" type function that gives the distribution of group types as a function of allele frequencies. This is simply an extension of the method used in classical population genetics to model the effects of selection on genotypes in terms of allele frequencies.

Species, however, clearly do not "reproduce" in this manner. Each new reproductively isolated population is derived from one and only one parent population. As a result, the distribution of group phenotypes in one generation is a function of the distribution in the previous generation (Wade, 1978). Although this pattern of reproduction makes modelling more difficult, we shall see that it actually increases the potential for species selection to influence evolution (Slatkin & Wade, 1978).

The way in which species reproduce, and the vast differences between the generation times of individuals and species, also makes it natural for us to define species level fitness as distinct from that of individuals. Once again, this deviates from most group selection models, which measure the influence of group level properties on the fitness of the individuals in the group. In such models, the fitness of a group measures the number of individuals that the group contributes to a migrant (or mating) pool (Uyenoyama & Feldman, 1980). Group selection in such cases is taken to mean that there is some property of the group that uniformly influences the reproductive output of its members. This is the sort of model used to study kin selection (Michod, 1982) and in discussions of the interdemic selection phase of Wright's shifting balance theory (Wright, 1977). (It is worth noting, though, that the shifting balance theory does not strictly require any group level property uniformly influencing the fitness or migration probability of individuals; it thus need not represent an example of group selection.)

Defining Species

For purposes of this discussion, a species is defined as a population of individuals that is reproductively isolated from other such populations over a period that is long relative to the time that it would take for a newly arisen allele to go to fixation by drift. (This last condition simply ensures that the population is isolated for a long enough time that we can observe some evolutionary dynamic within it.) This is, an approximation, as the amount of gene flow between populations is a continuous variable. It is, however, a good approximation for the purposes of studying the effects, on evolution, of differential splitting and extinction of lineages. I use the word "species", rather than "reproductively isolated population", not only because of the awkwardness of repeatedly using the latter term, but also because I believe that most of the examples of "species selection" in the paleobiological literature (where the topic is most often brought up) are examples of this.

Although I will focus on sexual organisms, the results are the same for those that reproduce asexually. In this case, the units of interest are populations of individuals that interact with one another such that the frequency of some strategy within a population can influence the probability of that population either splitting or going extinct. Also, it must be meaningful to think of a new variant arising within such a population and supplanting alternate strategies. This is similar to the idea of "demographic exchangeability" invoked by Templeton (1989) to define asexual species. (I am not arguing that these species definitions should supplant all others in all contexts, only that they are the appropriate ones for modelling multilevel selection. To

the extent that other definitions, particularly those used by taxonomists, differ from these, they are simply estimators of the actual units on which selection acts; more on this later.)

The groups, sexual or asexual, described above are defined by internal interactions between their component members. Note that this does not require that they be monophyletic. This is worth elaborating on, as some authors have argued for the idea of "clade selection" (Stearns, 1986; Williams, 1992) as a way to organize our thinking about selection above the level of individuals. I shall argue that this concept actually illustrates a problem that has hindered the development of a theory of species selection; the things on which selection acts are sometimes similar to, but not the same as, the things on which taxonomists focus.

Consider the population of asexual organisms whose progress through time is shown in Fig. 1. A new mutant arises that reproduces more frequently than its neighbours, and starts to spread. After it reaches some intermediate frequency, we look at the population and note that it contains a monophyletic group that bears a unique synapomorphy that increases the rate at which the group grows. It is clear, though, that this is not a case of clade selection, but rather of selection acting among individuals that happens, in this case, to favour all the members of a clade. If a back-mutation rendered one member of the group a slow reproducer,

the mechanics of selection would not change, even though the set of individuals favoured would no longer be monophyletic.

Now imagine that the fast reproducers in Fig. 1 derived their high fitness from some interaction between them. For example, the fitness of an individual might increase with the number of similar individuals. In this case, there is a group level property (group size, not definable in an individual) that influences the per capita growth rate of each of the groups members. Once again, a back-mutation that rendered the group paraphyletic, or an independent mutation elsewhere that rendered it polyphyletic, would have no impact on our assessment of the mechanism involved. The interaction among the group of individuals that express the character determines how fast that group grows, regardless of how its component individuals got the character or how many have lost it.

In short, selection tends to act on things based on their current state, not what they were doing in the past. Clades are defined by how their members are related as we look back in time, not by how they interact now. The only meaningful agent of clade selection would thus be something that could look back and "see" clade level properties, such as topology. Barring a deranged systematist with something against certain clade shapes, and the wherewithal to impose extinction at will, such selective agents are probably rare.

The Model

I shall concentrate on cases in which species selection is opposed by selection between individuals. This is not to say that this is always the case; as I mention later, the two processes may sometimes cooperate in important ways. The conditions that I shall set out, however, are those that species selection must meet if it is to play more than a supporting role in evolution.

Because species do not reproduce via a "migrant pool", but rather undergo a process akin to fission, we cannot model species selection by tracking the frequency of alleles across generation. Instead, we must study the dynamics of a distribution of species types over time (similar to that used by Levins, 1970). This requires the concept of a species phenotype, which I define here as the frequency of a particular type of allele or individual within a species. This is a species level property (not definable in an individual) that can influence the probabilities of either speciation or extinction. For example, the frequency of individuals that disperse over great distances before mating will influence the rate of gene flow between different parts of the species' geographic range, and thus poten-
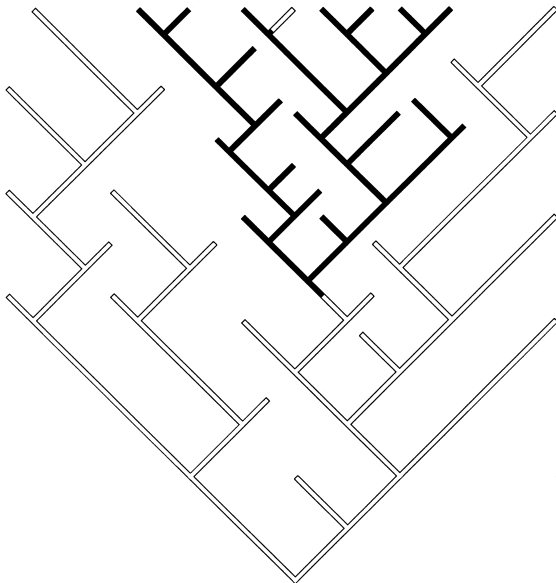

FIG. 1. A clade of asexual organisms, or a phylogeny of any units that reproduce by fission. The solid lines represent individuals that have some character that increases their rate of reproduction. This character is in the process of spreading through the clade. See text for discussion.

tially influence the rate at which new reproductively isolated populations form.

Defining species phenotype in this way, selection between individuals causes the phenotype of a species to change over time. Individual selection is thus, in a way, analogous to the process of development within an individual; the species' phenotype changes due to deterministic interactions between its component parts. For selection at a single locus with two alleles, the change in a species' phenotype (ϕ) is simply the change in allele frequencies within it, and thus satisfies

$$\frac{\mathrm{d}\phi}{\mathrm{d}t} = s\phi(1-\phi)[\phi + h(1-2\phi)] + u(1-\phi) - v\phi \quad (1)$$

(Ewens, 1979). Here, s is the within-population selection coefficient, h is the degree of dominance, and u and v are the forward and backward mutation rates, respectively (see Appendix for solutions). I shall focus on a single locus with selection favouring one or the other homozygote ($0 \leqslant h \leqslant 1$). Alternately, setting $h = 0.5$ and doubling the value of s, the same equation governs the evolution of a phenotypic character in an asexual population.

Figure 2 shows the species "life cycle" that I am considering. New species are formed when a set of individuals becomes reproductively isolated from its conspecifics. Once a new species is formed, selection between its members acts according to eqn (1). After τ individual generations, a new round of speciation takes place. I shall refer to this time from the formation
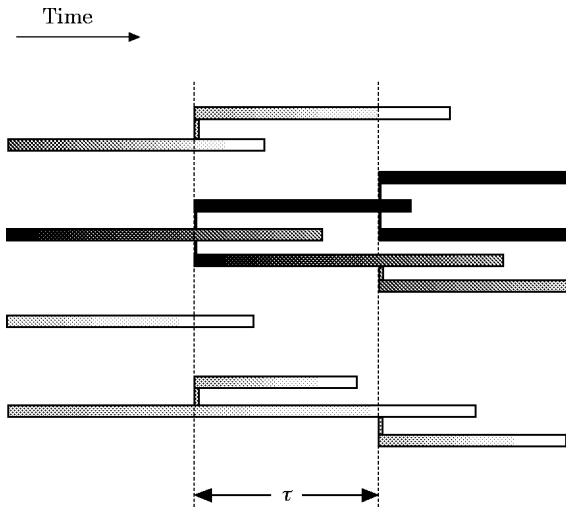

Time

FIG. 2. Simultaneous selection within and between species (lineages). Shading indicates the frequency of some allele within each lineage. White indicates fixation of the allele favoured by individual selection; black, fixation of the allele favoured by species selection. Any one lineage tends to become lighter over time, due to selection within it. Darker lineages, however, speciate more often. Speciation can occur every τ individual generation, while species may become extinct at any time.

of a species to the next round of speciation as a single species cycle. Note, however, that a single lineage may persist for more than one such cycle.

Consider a locus with two alleles, A_S and A_I, such that selection between individuals favours A_I while selection between species favours those with a high frequency of A_S. If each newly isolated species is made up of N individuals, then there are $2N+1$ possible phenotypes among newly formed species. We can arrange all species into a finite number of classes by defining species class i as the set of all species that started out with i copies of the allele favoured by individual selection (A_I). Letting $n_{i,k,}$ be the number of species in class i that have survived for k speciation cycles ($k\tau$ individual generations), the vector, $g_i = (n_{i,0}, n_{i,1}, n_{i,2}, \ldots)^\mathrm{T}$ identifies all the members of this species class (T indicates transposition). Combining classes, the vector $\mathbf{G} = (g_0, g_1, g_2, \ldots, g_{2N})^\mathrm{T}$ defines the distribution of all possible species phenotypes.

Let $w_{j,k}$ be the probability that a species in class j avoids extinction during the k-th speciation cycle since its formation, $f_{j,k}$ be the expected number of daughter species produced by those species in class j that persists for this time, and $P_{i,j,k}$ be the proportion of those daughter species that are in class i. Treating each new species is an unbiased sample of individuals from a parent population, and letting $\phi_{j,k}$ be the phenotype of class j after k species cycles ($\phi_{j,0} = j/2N$), then this term is given by:

$$P_{i,j,k} = \binom{2N}{i} \phi_{j,k}^i (1 - \phi_{j,k})^{2N-i}. \quad (2)$$

After both within- and between-species selection, the new vector, $\mathbf{G}'$, is given by

$$\mathbf{G}' = \mathbf{R} \cdot \mathbf{G} \quad (3)$$

where $\mathbf{R}$ is a transition matrix with elements r_{ij} specifying the rate at which species in class j produce daughter species in class i.

A consequence of selection between individuals is that it is very rare for a daughter species to start out with fewer alleles of the type favoured by individual selection than its parent species did. This is because, by the time the daughter species forms, the parent species' phenotype has shifted in the direction favoured by individual selection. There is thus a bias in the rules of inheritance at this level: offspring tend to look consistently different from what their parents looked like at the same stage in the cycle. This effect is seen in Fig. 3, which shows a distinctly nonlinear regression of offspring phenotype on that of their parents.
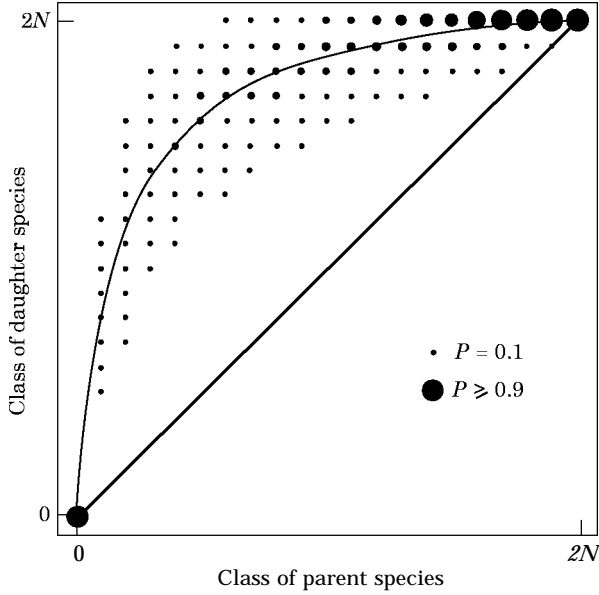
FIG. 3. Probability of drawing a daughter species with a particular phenotype as a function of the phenotype of the parent species when it initially formed. The thin line is the phenotype of the parent after τ individual generations. The distribution is bowed up because within-group selection changed the phenotype of the parent before they produced progeny. The size of the dots represents the probability associated with each point, and these probabilities are identical to the $P_{i,j,1}$ values in eqn (3). In this example, $s = 0.01$, $N = 10$, $u = 10^{-6}$, $\tau = 500$.

Thus, $r_{ij} \approx 0$ for $i < j$. This greatly simplifies the analysis of eqn (3), since the transition matrix **R** is nearly triangular, its eigenvalues are very closely approximated by those of the diagonals, r_{ii} (see Appendix). If a species can persist through many speciation cycles, then the r_{ii} are themselves matrices given by:

$$r_{ii} = \begin{bmatrix} w_{i,0}f_{i,0}P_{i,i,0} & w_{i,1}f_{i,1}P_{i,i,1} & w_{i,2}f_{i,2}P_{i,i,2} & \ldots \\ w_{i,0} & 0 & 0 & \ldots \\ 0 & w_{i,1} & 0 & \ldots \\ \cdot & 0 & & \cdot \\ \cdot & \cdot & & \\ \cdot & \cdot & & w_{ij}\ 0 \end{bmatrix}$$

(4)

The entries in this matrix represent the contributions to species class i of species in class i that have persisted through different numbers of cycles.

Note that the matrix in eqn (4) has the same form as the Leslie Matrix used to model growth of an age structured population. It appears here because the probability that a species with initial phenotype i will produce a daughter with the same phenotype ($w_{i,}f_{i,.}P_{i,i,j}$) changes as individual level selection within the parent species causes its own phenotype to change;

just as the fertility of an organism changes throughout its life cycle. This further hints at an analogy between individual selection within a species and development of an individual.

Because those species that are fixed for one or the other allele have the highest heritability (Fig. 3), the two largest eigenvalues of the matrix **R** are very closely approximated by those of the submatrices, r_{00} and r_{2N}. I shall refer to these as λ_s and λ_i respectively. λ_s is the rate at which species that are close to fixation for the allele favoured by between-species selection (species class 0) produce daughter species that are also close to fixation for this allele, and is defined by:

$$\sum_{x=1}^{\infty} W_{0,x}f_{0,x}P_{0,0,x}\lambda_s^{-x} = 1.$$

(5)

Similarly, λ_i is the rate at which species that are nearly fixed for the allele favoured by individual selection produce species nearly fixed for that allele. It is defined by:

$$\sum_{x=1}^{\infty} W_{2N,x}f_{2N,x}P_{2N,2N,x}\lambda_i^{-x} = 1.$$

(6)

Assuming that the frequency of the allele favoured by individual selection goes from fixation to mutation–selection equilibrium (which is very near fixation) in one speciation cycle, λ_i is equivalently given by

$$\lambda_i = w_{2N,0}(f_{2N,0}P_{2N,2N,0} + 1).$$

(7)

The largest of these is the dominant eigenvalue of the matrix **R**, thus, if

$$\lambda_s > \lambda_i,$$

(8)

then species selection can cause a particular species class to increase in frequency when rare, within a clade, even in the face of opposing selection between individuals. If this condition is not met, then selection between individual organisms completely swamps out the effects of selection between species (Fig. 4). (The equilibrium distributions shown in Fig. 4 are generated using the full matrix, **R**, without assuming that $r_{ij} \approx 0$ for $i < j$.)

Again, we can make this two-state approximation because of the bias in species inheritance illustrated in Fig. 3. Selection between individuals ensures that species that start out with an intermediate frequency of the allele in question ultimately contribute almost exclusively to species in class $2N$.

Discussion

Using eqn (8), we can investigate the influences of ecological factors (through their impact on N, w, f
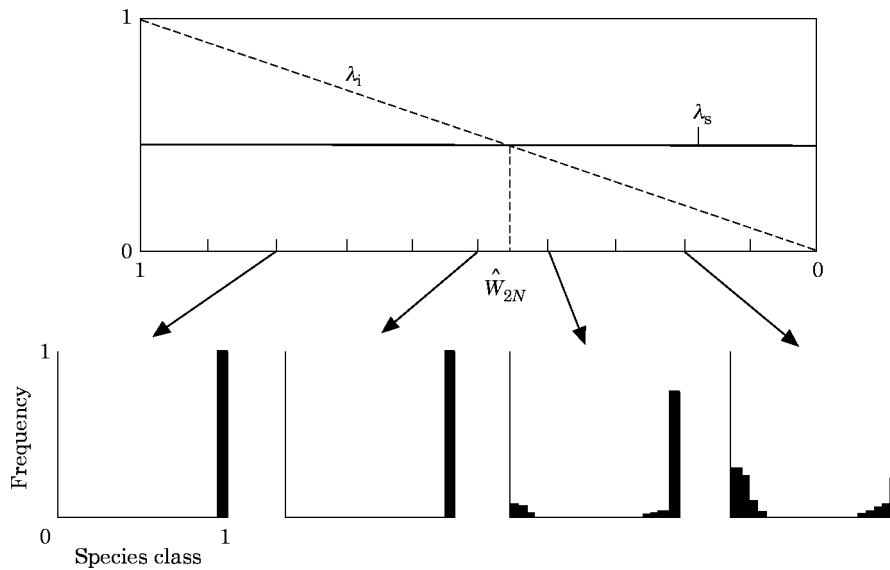
FIG. 4. The equilibrium distributions of species phenotypes (the four distributions below) resulting from different values of λ_i and λ_s. The x-axis plots the fitness of species fixed for the within-species favoured character (i.e. those that are being selected against by species selection). $\hat{W}_{2N}$ is the probability that such a species survives one speciation cycle. In this example, species fitness drops off linearly with increasing frequency of the allele favoured at the individual level. The result, however, is dependent only on the fitness of those species that are fixed for one or the other alleles. For this example: $s=0.1$, $h=0.5$, $N=20$, $\tau=500$ and $u=10^{-6}$.

and τ), and organismic properties (u and h) on the efficacy of species selection. I shall focus on the influences of the time between speciation events (τ) and the mutation rate (u). I will assume individual selection coefficients in the range $s=10^{-3}$–10^{-2}, weak to moderate selection, and ask under what circumstances species selection is effective at opposing selection between individuals.

The time between speciation events (τ), measured in units of individual generations, is among the most important parameters in the model; it is also the most difficult to estimate. Because we define fossil species solely on the basis of morphology, the rate at which new species are seen to arise is determined by both the rate of formation of reproductively isolated populations (what we are concerned with here) and the probability that such a population both persists long enough to leave a discoverable fossil record, and diverges sufficiently to be identified as a distinct species by some future taxonomist. The rate of speciation, as calculated from the fossil record, is thus a function of the rates of both origination and extinction of reproductively isolated populations, and will vastly underestimate the rate at which such populations arise. Speciation rates calculated from the fossil record will thus overestimate the true value of τ.

We can estimate one piece of this error by studying geologic or climatic events that must have fragmented existing populations, and asking how often these produced what taxonomists have deemed new species.

Such a study, by Cronin & Ikeya (1990), found that, for fossil Ostracods, only 1–2% of isolating events produced taxonomically distinct species. We can thus guess that speciation rates from the fossil record can underestimate actual splitting rates by two orders of magnitude. This said, such estimates can at least provide a conservative test to tell us if the conditions ever exist under which species selection can be an effective evolutionary mechanism.

Table 1 and Fig. 5 show that for at least one known lineage, that leading to modern Asian elephants, τ is sufficiently small that, even without correcting for isolation events that do not produce new species,

TABLE 1

Values of τ for some groups for which it is particularly high

Genus	S/mv	Generations	τ
Elephas	2.00	>18	2.7×10^4
Alcelaphini	2.14	5	9.4×10^4
Phacochoerus	2.30	4	1.1×10^5
Loxodonta	0.40	>20	1.2×10^5
Ammonoidea	1.40	5	1.4×10^5

S/my is the rate of appearance of new taxa per million years. The value for *Elephas* is sufficiently small that species selection could influence the evolution of characters with mutation rates of the order of 10^{-6} and individual selection coefficients of 10^{-3}. Similar individual selection could be overcome in the other groups of characters with mutation rates of the order of 10^{-7}. Rate data for mammals are from Rosenzweig & Vetault (1992) and Vrba (1987). Data for ammonites are from Stanley (1990). Generation times are for living representatives of the mammal group (Nowak, 1991), and for *Nautilus* as the closest modern analogue of Ammonites (Ward, 1983).
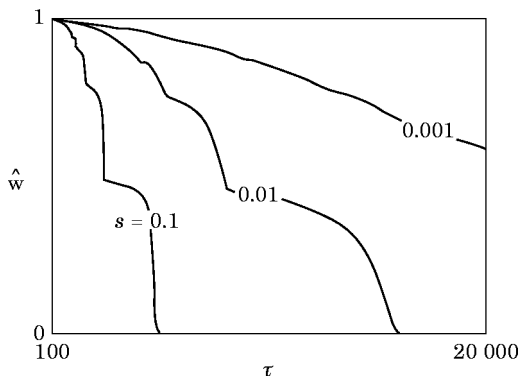
FIG. 5. The strength of species selection necessary to influence evolution as a function of τ. The different curves represent different values of the within-species selection coefficient (s). $\hat{w}$ is the relative fitness of species fixed for the allele favoured by individual selection (those fixed for the alternate allele are assigned a fitness of 1). A small value of $\hat{w}$ thus corresponds to strong species selection. For a particular value of s, species selection is effective only under the curve for that value. In this example: $h=1$, $N=20$, $u=10^{-6}$. The stepped appearance results from the fact that at each round of speciation, the parent species is some whole multiple of τ old. The last, and largest, "step" represents the contribution of the newest members of class 0; the next step represents the contribution of those members of class 0 that have persisted through one cycle already; and so on.

species selection could influence the evolution of characters with mutation rates of the order of 10^{-6} per generation, complete dominance, and within-species selection coefficients of the order of 10^{-3}. (Though only one species exists now, speciation rates in the lineage leading up to it could still have been high.) For a number of other groups, τ is small enough that characters with mutation rates of the order of 10^{-7} could be maintained by species selection. These examples show that conditions do sometimes exist under which species selection can be an effective evolutionary mechanism (if we reduce the values in Table 1 by a factor of 10, much less than suggested by the Ostracod example above, then all of the groups listed become candidates for species selection). This example also draws our attention to the fact that, if isolation events occur on a time-scale independent of an organism's lifespan, then lineages made up in organisms with long generation times are more likely to be influenced by species selection than those composed of short-lived organisms.

Figure 6 further illustrates the influence of mutation rate on the effectiveness of species selection. If mutation rates are larger than about 10^{-4} per generation, even very weak selection between individuals can nullify the effects of species selection. Although per-locus mutation rates are generally much smaller than this (10^{-6}–10^{-5} per gamete per generation), the total phenotypic mutation rate for quantitative or polygenic characters may be much

higher, simply because such characters are influenced by many loci. This is significant because body size, which has often been cited as a prime candidate for the effects of species selection (Levinton, 1988), is a classic polygenic trait that is influenced by more than 100 loci in organisms as disparate as mice and the flour beetle *Tribolium*. The rate at which size variants arise in a population is thus likely to be so high as to preclude the effects of species selection unless body size is neutral with respect to individual fitness. Conversely, characters with particularly low mutation rates, or those that require mutations at separate loci that interact epistatically, are particularly susceptible to the influence of species selection.

This model highlights a number of conceptual issues in the general theory of selection that are not readily apparent when we study only selection between individuals. In particular, it shifts us away from the question of what biological entities can be units of selection (to which the answer is: almost anything) and instead focuses our attention on what properties a particular kind of unit must have if selection between those units is to influence evolution.

The transmission rules, describing inheritance at whatever level we are studying, clearly have a strong influence over the efficacy of selection at that level. Not surprisingly, the most important factor here is the probability that the progeny resemble their parent at the same stage in the cycle. What is surprising is that, if there is also selection at some lower level, the expected phenotype of the progeny may not be that of their parents. That is, there may be biased inheritance such that, on average, daughter groups look consistently different than their parents did at the same stage. In such a case, selection is most efficient when the variance in phenotype between the daughter groups is high. This increases the probability that groups that start out near some group selection optimum produce
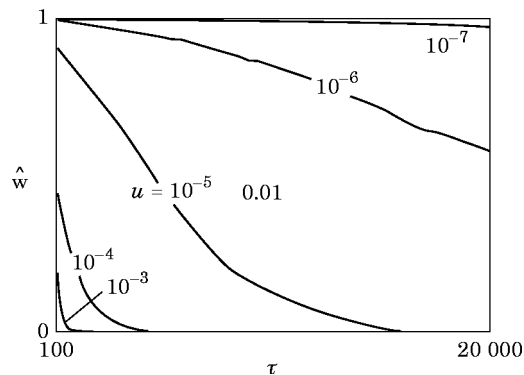

FIG. 6. Same as Fig. 4 except that here the different curves show the results for different mutation rates (u). Here, $s=0.001$.

some progeny that are also near that point, even though individual level selection is always moving them away. The mechanics of group formation, which strongly influence the variance within and between daughter groups (Whitlock & McCauley, 1990), is thus a major determinant of the efficacy of group selection.

This is why group selection in general is a more potent evolutionary factor when groups reproduce by fission than when they contribute to a common migrant pool. Fission increases the probability of drawing a daughter group that is fixed for the character favoured by group selection. I have assumed above that each daughter group is a random sample of individuals from its parent; this gives a conservative estimate of the efficacy of species selection. Any spatial structure within a population will tend to increase the likelihood of drawing a homogeneous sample, and thus increase the power of selection between species to influence evolution.

The effects of spatial structure should become most important in the case of colonies, such as those of corals and Bryozoans, that are composed of many individuals attached in a rigid framework. When new colonies form through the fragmentation of larger ones (as is often the case with some reef-building corals), each fragment is composed of closely related individuals. Thus, if a variant has arisen in a colony due to "somatic" mutation, there is a good chance that a fragment can form that is composed principally of that variant. Colony level selection in thus much more efficient when colonies are structured and reproduce by fragmentation than it would be if new colonies were drawn as a random sample of individuals from a parent.

Modelling species selection also makes the entire issue of group selection more clear cut. Much of the confusion surrounding the units of selection has resulted from the fact that we can sometimes collapse the results of processes at different levels into one term, making it look as though selection is acting at only one level. For example, inclusive fitness combines processes acting at the level of the individual (number of offspring) with those at the level of the interacting family group [adding in the individual's influence on others' reproduction, devalued appropriately, and (though it is often forgotten) subtracting the influence of others' actions on the individual in question]. This works because the generation times of individuals and family groups are the same, so we can combine processes at different levels and still calculate the allele frequencies in the next generation. In the case of species selection, we cannot hide the different levels in this way. Because species' generation times are so much longer than those of individuals, we are forced to recognize the two processes as distinct.

I have focused on selection between individuals as the main mechanism of evolution within species. Genetic drift is also relevant to the efficacy of species selection, but in a different way. If a species is close to fixation of an allele favoured by species selection, then genetic drift will increase the likelihood that it will produce a daughter species that is in fact fixed for that allele. Drift thus increases the heritability of this condition and reduces the ability of individual selection to move the system away from it.

Species selection is least efficient when acting on characters that are not common in any population. It is thus more efficient at maintaining characters once they are established than at establishing them in the first place. This is especially true for complex morphological adaptations that may involve a number of separate genetic changes, such as demersal larvae (Jablonski & Lutz, 1983). As discussed above, though, such characters may be good candidates to be influenced by species selection once they get started in some population. This hints at an important potential interaction between selection within species and selection between them. Complex characters may initially increase in frequency due to temporary individual selection favouring them within some population. Once common, they are good candidates to be maintained by species selection, even in the face of varying individual selection regimes, because of the low rate at which they are lost as a result of mutation. The most significant consequence of species selection may therefore not be the appearance of novel morphological characters, but the persistence, over long stretches of geologic time, of some complex characters that arise rarely and are only occasionally favoured by selection between individuals.

The relationship between individual and species selection is thus a complex one. While selection between individuals can eat up variance between species, it may be necessary to construct complex adaptations and get them to a frequency at which species selection can maintain them. Thus, while we may be able to "decouple" the agents of selection between species from the agents of selection within them, we cannot decouple their consequences for evolutionary dynamics.

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APPENDIX

If there is no dominance ($h = 0.5$) and $u = v$, then eqn (1) has the solution

$$\phi_t = \frac{s - 2u}{2s} - \frac{\sqrt{s^2 - 4u^2}(1 + Ce^{\sqrt{s^2 - 4u^2}t})}{2s(1 - Ce^{\sqrt{s^2 - 4u^2}t})}.$$

Where:

$$C = \frac{2s\phi_0 - s + 2u + \sqrt{s^2 + 4u^2}}{2s\phi_0 - s + 2u - \sqrt{s^2 + 4u^2}}.$$

If s is small, then eqn (1) approximates the discrete process:

$$\Delta\phi = \frac{s\phi(1 - \phi)[\phi + h(1 - 2\phi)] + u(1 - \phi) - v\phi}{\phi^2(1 + s) + 2\phi(1 - \phi)(1 + hs) + (1 - \phi)^2}$$

which can be iterated for τ time units to provide results when $h \neq 0.5$.

To estimate the accuracy of assuming that the matrix R is triangular: let μ_s and μ_i be the actual eigenvalues that λ_s and λ_i are approximating. Then if $\mathbf{v}$ is a horizontal vector with all elements are equal to 1, then using Girshgorin's theorem (Golub & Van Loan, 1989) we can write:

$$|\mu_s - \lambda_s| \leqslant \sum_{j=1}^{N} vr_{0,j}v^{\mathrm{T}}$$

and:

$$|\mu_i - \lambda_i| \leqslant \sum_{j=0}^{N-1} vr_{j,2N}v^{\mathrm{T}}.$$

The right-hand sums in these equations are just the sums of the non-zero off diagonal elements of R. Calculation of these values and simulations show that the approximation used in the text is accurate for individual selection coefficients down to 0.005 with $\tau > 500$ or down to 0.001 with $\tau > 3000$.