cess could selectively filter out the high spatial frequencies responsible for aliasing but not the low-frequency alias they have already spawned. These high frequencies that are not themselves resolved can still leave a clue to their existence in the moiré patterns they produce. One solution to the aliasing problem is to remove the offending spatial frequencies from the image prior to the sampling process. Low-pass optical filtering tends to protect human foveal vision in this way (*15*). Yellott (*9*) has pointed out a second way the visual system copes with aliasing: the irregularity of the cone mosaic smears aliased energy into a broad range of spatial frequencies and orientations, making it less easy to detect. Though spatial vision through the B cone mosaic must also benefit from sampling irregularity, our experiments show that the spurious energy produced by photoreceptor undersampling in one's own retinal mosaic can be visualized.

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Macroevolutionary Trends: New Perspectives on the Roles of Adaptation and Incidental Effect

Abstract. *Trends, long-term directional tendencies in evolution, are traditionally interpreted as selected for and adaptive. Alternatively, trends may be unselected effects of characters and processes within species: the effect hypothesis. Thus adaptations of organisms, varying among species, were selected for immediate fitness, but they may also incidentally determine different speciation and extinction rates and trends.*

A new concept of how the long-term patterns of evolution such as trends may come about, the effect hypothesis (*1*), focuses on a neglected potential of some characters and processes at genomic and organismal levels: the potential to determine differences among related lineages in net species increase. It suggests that differential species diversification and directional phenotypic trends in monophyletic groups (*2*) of sexually reproducing organisms may be nonrandom and yet not adaptive—that is, a particular trend need not be more adaptive, progressive, or successful than alternatives, although all evolution in component lineages may have been under the control of natural selection. In proposing direct upward causation (*3*) to deterministic sorting among species, and therefore to nonadaptive long-term patterns, the effect hypothesis differs from other models of macroevolution, such as the traditional synthetic concept (*4*), the species selection (*5–8*) and random (*9*) models, and the notion that trends are determined largely by intrinsically directed introduction of phenotypic variation (*10*).

Two aspects of trend evolution in monophyletic groups are (i) phenotypic divergence between early and late lineage end points and (ii) the differential increase in numbers of species. The net rate of increase in species in a monophyletic group R is $S - E$, where S is speciation rate and E is species extinction rate (*6, 7*); speciation refers only to lineage splitting. Mean divergence XY in particular characters may theoretically occur separately from or together with differential R. Punctuated equilibria (*5*) introduced the notion of linking divergence and diversity, and to the extent that a punctuated pattern predominates in a phylogeny, we cannot extrapolate notions of directional evolution within species to explain a divergence trend. Rather divergence must depend on variation in S, E, speciation direction, or permutations of them. The trend XY can result from a bias in the direction of speciation events (Fig. 1d) or an increase in R (Fig. 1h). In contrast, divergence trends evolved by "phyletic gradualism" (*5*) are not a function of S and E (Fig. 1, c and g). Punctuated equilibria forces us to consider not only the potential causes of origin and sorting of variation at the level of organismal phenotypes but also those among species. In the absence of a punctuated pattern we still need to explain differential species diversity.

Williams (*11*) suggested that adaptations of organisms, shaped by natural selection to perform particular functions, may have incidental effects that are not the direct consequence of selection. As explicitly argued (*12*) and generally accepted (*13*), speciation is usually an incidental consequence of the accumulation of genotypic and phenotypic differences between populations. To the extent that evolution is about the maintenance of adaptation (*11*), the environmental events that cause speciation may be seen as random accidents, the divergence away from a common fertilization system as disruption, relative to the existing adaptations in the parent species. Thus species are not adaptations, although the component organisms may be adapted, but effects (*12, 14*).

If species commonly result as effects of evolution at lower levels, then it is probable that differential S does as well. If there are characters of genomes and organisms that confer characteristic probabilities of speciation and if such characters in related species differ, then S will differ. Combinations of S and E may vary across a monophyletic group to cause trends toward higher R (Fig. 1, e–h). Suggestions of characters, adaptations, or others, which could potentially effect differential R, focus on susceptibility to new genomic and phenotypic vari-

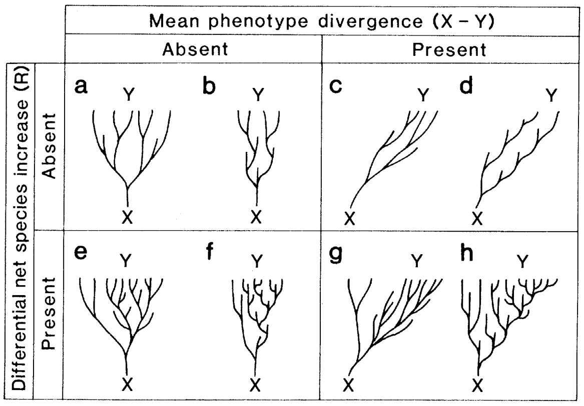

Fig. 1. Phylogenetic trees with phenotypic characters varying along the horizontal axes, and time along the vertical axes. (*b, d, f,* and *h*) Cases show a pattern of punctuated equilibria (*5*); (*a* and *b*) cases are not trends; (*c* and *d*) cases are trends only in terms of phenotypic divergence; and (*e* and *f*) cases are trends only in terms of differential R; in trends *g* and *h* divergence occurs together with increase in R. (*e* to *h*) Increasing S overwhelms increasing E and results in differential, positive R, but these cases could also have been drawn to show increasing R as a result of decreasing E overwhelming S.

ation (*10, 15*), on the spread of mutations without selection (*16*), or on different susceptibilities to directional selection. I suggested (*1, 17*) that features such as adaptations that confer breadth of resource use may be characters of organisms, with incidental but deterministic effects that translate to patterns of among-species evolution. Organisms that can use resources in alternative environments (such as a lineage may encounter through time) are subject to less directional selection, and their lineages to lower S and E. Specialist organisms, whose resources disappear as environments change, are more subject to directional selection and range fragmentation and their lineages to high S and E (*17*).

Many regard organisms as units of selection (*18, 19*). Several caution that assertion of an adaptation requires a history of selection (*11, 12, 20, 21*) and that adaptation should be recognized at levels higher than the organism only if demanded by the evidence (*11, 12, 22, 23*). If mutants increase the fitness of organisms, then their spread in some or other groups (and any resultant differential fate of groups) need be attributed only to selection of genotypes and phenotypes (*11, 19, 22*). It would be as trivial to describe such cases as group selection as to describe species selection as the differential reproduction or survival of species that are determined directly by selection of organisms. The point is that group or species selection is not the only possible cause of nonrandom patterns among groups or species. Insofar as selection is the cause, theoretically it may be selection at the group and species level or at lower levels, or both.

The effect hypothesis states that differences between lineages, in characters of organisms and their genomes, may determine a pattern of evolution among species in a monophyletic group. Take the case where such characters are organismal adaptations. They were not selected for promoting or retarding S, nor for avoiding species extinction in the face of future environmental change. Natural selection acts for "reproductive performance regardless of the effect on long-term population survival. It is not a mechanism that can anticipate possible extinction and take steps to avoid it" (*11*, pp. 31 and 32). Although not selected for such functions, organismal adaptations may determine S and E. Adaptations may have incidental effects within species (*11*). The translation of effects to patterns among species is the focus of the effect hypothesis of macroevolution. This proposal does not require punctuated equilibria: differential R may occur as an effect in gradual phylogenies (Fig. 1, e and g). To the extent that a punctuated pattern predominates, long-term divergence may result as an effect (XY in Fig. 1h). Originally (*1*) I used Wright's suggestion (*24*) that the direction of speciation events may be random with respect to trend direction. But this condition is not necessary, since effect evolution may superimpose on biases in speciation direction.

Many radiations show positive correlations of S and E (*6, 7, 17*). This result is expected, for instance, if breadth of resource use of organisms dictates both rates (*1*). If the trend shown in Fig. 1h resulted by effect, then (i) the pattern is punctuated, (ii) the directions of speciation events do not on their own account for divergence XY, and (iii) the trend results in spite of increasing E from left to right because increasing S overwhelms E. This trend is not adaptive (*25*). Another kind of trend would result if only (i) and (ii) apply, but decreasing E is the important element determining the trend. Such a trend would be toward better-adapted organisms (*26*).

Causes of trends may be especially well studied in monophyletic groups with a good fossil record and extant survivors that are still in a phase of radiation. Particular hypotheses of effect evolution can lead to precise predictions of how character variation should correlate with S, E, R, and trends. These can be tested by comparing phylogenetic hypotheses with the distribution of variation in genetics, karyotypes, population genetics, morphology, ecology, geographic distribution, and so on among extant and, where possible, extinct species. The hypothesis is supported by data from several Miocene to Recent mammal groups (*17*).

Before 1980, species selection stressed two themes (*5–8*). First, differential survival of species, or higher E of the less well adapted species, was regarded as dominant in accounting for a trend. Thus even where brief consideration was given to the possibility that high S might overwhelm E in producing a trend, high S (as documented in the fossil record) was seen as a function of the survival rate of incipient and new species (*7*, p. 198; *27*). Second, species were interpreted as owing their success at the pinnacle of a trend to adaptive improvements that were more efficient, competitive, and advanced than those of the losing species (*28*). Species selectionists implied that more species equates with more organisms and genes and did not address the possibility of intrinsic determination of S. In this model species are irreducible units of selection; hence species-selected macroevolution is seen as decoupled from microevolution (*6, 7*). The distinction between species selection and effect macroevolution does not lie in whether E or S is stressed as determining trends, but in the level or levels at which aptation (*21*) and selection are identified.

I suggest that we theoretically separate two processes: one in which species' aptations (*29*) result in their selection, called species selection; the other in which Darwinian selection of organisms and other lower level processes simply determine differential R and patterns among species, called effect macroevolution. Species selection requires species as units of selection and species aptations that are not merely the simple additions of organism adaptations or other characters; thus resultant trends are adaptive, and the process is not reducible to natural selection within species. The effect hypothesis requires no units of selection above the level of organisms and no aptation above the level of organisms; any resultant trends need not be adaptive, and the process is reducible to combinations of long-recognized microevolutionary processes. If we follow widely accepted analyses of what may not be termed group selection (*11, 22, 23*), then consistency demands recognition of effect macroevolution as separate from species selection.

There are suggestions that the frequency of certain variants available at genetic and phenotypic levels may be intrinsically determined (*10, 15*). The effect hypothesis translates this notion to variation among species. It suggests that life's diversity patterns, and through them some long-term directional tendencies, may be incidental nonadaptive consequences. The effect hypothesis is simpler and makes fewer assumptions than the hypothesis of species selection. The onus is on those who assert group selection in any particular case to show that the concept is demanded by the evidence—that is, that selection of genotypes and phenotypes or other lower level processes do not provide a sufficient explanation of the deterministic pattern among groups. The effect hypothesis is of particular relevance to analyses of species diversity in ecosystems. It recognizes hierarchy of biological organization. But a hierarchical approach, which addresses the causes of sorting among species, cannot "negate the importance of population level phenomena" (*30*). Testing for causes of macroevolutionary pattern may require studies involving many subdisciplines from genetics to paleontology.

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27. A comparable *S* has been suggested for generalist and specialist species, with a high *E* of new generalist species resulting from large niche overlap (*8*, p. 310).
28. Species-selected trends represent new and improved efficiency (*5*); see also Stanley (*7*, p. 184).
29. Just as a claim of group aptation requires special argument (*11, 22*), so does a claim of species aptation (*26*). If all organisms in a species are black, black color is a species character. If black organisms are subsequently removed by selection, but those of different color in a related species survive, this is differential species extinction. Selection of organisms is enough to account for events, and there is no need for concepts of species aptation and selection.
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Interactions Among Converging Sensory Inputs in the Superior Colliculus

Abstract. *The responses of superior colliculus cells to a given sensory stimulus were influenced by the presence or absence of other sensory cues. By pooling sensory inputs, many superior colliculus cells seem to amplify the effects of subtle environmental cues in certain conditions, whereas in others, responses to normally effective stimuli can be blocked. The observations illustrate the dynamic, interactive nature of the multisensory inputs which characterize the deeper laminae of the superior colliculus.*

One assumption underlying neurophysiological studies of the superior colliculus has been that detailing the response properties of its constituent cells in the laboratory will give us insight into how these cells function under more "natural" environmental conditions. Investigators have usually determined the characteristics of a given superior colliculus cell by examining its responses to a modality-specific (for example, visual) stimulus whose physical parameters are systematically varied. In this manner, the investigator identifies the physical characteristics of those stimuli likely to have optimal access to the circuitry of the superior colliculus and, therefore, most likely to evoke an orientation response (*1*).

Table 1. Frequencies of superior colliculus neurons from cat (59 cells) and hamster (49 cells) by type of interaction (*9*) and laminar distribution (*8*). Numbers in parentheses are percentages.

Interaction	Cell location		Totals
	Superficial laminae	Deep laminae	
Enhancement	0	26 (29.2)	26
Depression	0	21 (23.6)	21
None	19 (100)	42 (47.2)	61
Totals	19	89	108

Yet during normal behavior an animal is confronted with a variety of simultaneous stimuli from different sensory modalities. The likelihood of an orientation response may depend as much (if not more) on the combination of stimuli as on the normal effectiveness of any individual stimulus. It is possible that this behavioral phenomenon occurs because the influence of a sensory stimulus on a given neuron can vary in the presence of