

Species Selection: Theory and Data

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Abstract

Species selection in the broad sense—also termed species sorting—shapes evolutionary patterns through differences in speciation and extinction rates (and their net outcome, often termed the emergent fitness of clades) that arise by interaction of intrinsic biological traits with the environment. Effect-macroevolution occurs when those biotic traits, such as body size or fecundity, reside at the organismic level. Strict-sense species selection occurs when those traits are emergent at the species level, such as geographic range or population size. The fields of paleontology, comparative phylogenetic analysis, macroecology, and conservation biology are rich in examples of species sorting, but relatively few instances have been well documented, so the extent and efficacy of the specific processes remain poorly known. A general formalization of these processes remains challenging, but approaches drawing on hierarchical covariance models appear promising. Analyses integrating paleontological and neontological data for a single set of clades would be especially powerful.

Aggregate traits:

species properties that are characteristics of individual organisms (body size) or combined measurements of organisms (mean body size)

INTRODUCTION: HIERARCHY AND EVOLUTION

Complex systems naturally fall into hierarchies. Among the many hierarchies found in biological systems, the one incorporating genes, bodies, populations, species, and clades has incited the greatest controversy, centering on the dynamics of units at different levels and the consequences. Selfish or parasitic DNA sequences were quickly seen in this hierarchical light, subject to selection and other evolutionary forces within the genome and with effects cascading both to and from higher levels. In contrast, the potential for analogous processes operating on species within clades has had a longer but more troubled history. However, the view that differential speciation and extinction rates can shape evolutionary trajectories and trait distributions across clades is increasingly accepted theoretically and is supported by a growing but scattered body of data. Here I review the different definitions of species selection in the context of multilevel selection (MLS) theory, discuss potential approaches toward the still-incomplete formalization of species selection, and give an overview of the empirical evidence bearing on the operation of the processes that fall under the different concepts of species selection. I will not provide a full historical review, but discuss progress in developing operational approaches and an empirical basis for this aspect of MLS.

Most workers now accept that broad-sense species selection can occur in principle [including such early critics of different forms of MLS as Dawkins (1989), Williams (1992), and Maynard Smith (1998)]. The question is thus an empirical one: when does species selection occur, and how can we recognize it and quantify its effects? The growing acceptance of species selection (in the broad sense) as a potential evolutionary force derives in part from an expansion in the range of evolutionary questions being addressed. The focus is no longer so exclusively on changes in allele frequencies and how those might drive the origin of features such as eyes and horns, but instead it more actively includes the frequencies of such features among clades (how many species have horns), the fates of those features (how long do horns last, in evolutionary terms), and origination and extinction rates of species and clades (why do clades wax and wane, and do horns determine clade dynamics in some way, or they are carried along in association with other features). Simple extrapolation from organismic fitnesses cannot always fully account for the dynamics of clades (see overviews by Jablonski 2000, 2005, 2007, 2008a), and so hierarchical approaches, comprising several elements including species selection, have increasingly been invoked. This does not mean that organismic-level processes are unimportant, of course, but suggests that effects of scale and hierarchy also enter into the equation for long-term, large-scale evolutionary patterns.

SPECIES SORTING AND SELECTION

Emergent Properties and Emergent Fitness

The term species selection has been used in both broad and narrow senses, sometimes by a single researcher. In its original broad sense, species selection referred to the differential origination or persistence of species—together considered the emergent fitness of species within clades—owing to interaction with the environment. (By contrast, species drift can occur by differences in origination and extinction in the absence of environmental interaction, as noted below.) Early proponents were concerned mainly with differential survival of species on the basis of organismal, aggregate traits present in all members of the species, and many still favor this usage (e.g., Arnold & Fristrup 1982; Coyne & Orr 2004; de Vries 1905, p. 800; Eldredge & Gould 1972; Gould 2002; Gould & Lloyd 1999; Morgan 1903, pp. 462–64; Okasha 2006; Stanley 1975a, 1979; Wright 1956; and see Lloyd 1988, pp. 101–7, 2000; Lloyd & Gould 1993; Stidd & Wade 1995; Williams 1992, pp. 26–27). Because traits affecting speciation and extinction rates can reside at any hierarchical

level, organismic attributes such as body size or metabolic rate can promote broad-sense species selection as readily as species-level attributes such as geographic range or genetic population structure (emergent traits; see below). The key requirements are that (*a*) a trait exhibits little or no variation within species relative to the variation among species (see Gould 2002, pp. 664–65 for his clearest statement on this point), and (*b*) speciation and/or extinction covaries consistently across one or more clades with that trait. Mammalian body size is often viewed in this light: Species tend to exhibit modal sizes, and a cross-level discordance may exist in the evolutionary consequences of size in that short-term organismic selection might often favor larger body size (cf. Kingsolver & Pfennig 2004), but larger bodied species or clades may be more extinction-prone over longer time scales (e.g., Van Valen 1975, Van Valkenburgh et al. 2004). Of course, broad-sense species selection need not oppose selection at the organismic level, although this is analytically more tractable; selection might as readily operate in the same direction at multiple levels (see Grantham 1995, Lloyd & Gould 1993; such concordance assumes some intraspecific variation in a focal trait, which still could be modest relative to among-species variation).

An alternative approach applies the more general term species sorting to nonrandom differences in emergent fitness (i.e., broad-sense species selection), and attempts to specify the hierarchical level of the traits that confer those differences. Effect-macroevolution then signifies differential rates governed by organism-level—that is, aggregate—traits, whereas strict-sense species selection refers only to differential rates that are governed by emergent, heritable properties at the species level (see Damuth & Heisler 1988; Grantham 1995, 2001; Jablonski 1987, 2000; Vrba 1984, 1989; Vrba & Gould 1986). In Campbell's (1974) famous terms, for effect-macroevolution the focal level of selection is the organism, but upward causation to higher levels via effects on speciation or extinction probabilities can drive clade dynamics in unexpected ways, as in the body-size example above (see Vrba & Eldredge 1984, Vrba & Gould 1986). For strict-sense species selection, the focal level is the species, with downward causation influencing the frequencies of organismic traits among clades (a process termed species hitchhiking by Levinton et al. 1986) and upward causation again shaping overall clade composition. This narrower definition of species selection more stringently incorporates the classical recipe for evolution by selection codified by Lewontin (1970)—differential production or survival of units owing to interaction of heritable traits with the environment—and so requires the identification of both emergent species-level traits and their heritability among species.

Identifying emergent properties of species is not straightforward, and by some accounts emergent and aggregate traits are extremes on a continuum, depending on the complexity of the interactions among organism-level properties (and environmental effects, as in any phenotypic trait) in generating the species-level property (Okasha 2006; see also Wimsatt 2007, chapter 12). Just as we often think of selection as operating on phenotypes determined by the interaction of many genes (and the environment) rather than as operating solely at the genic level, the interaction of many factors to determine a geographic range size, a genetic population structure, or a level of intraspecific variation can yield an emergent property whose evolutionary effects are not reducible to any single organismic property.

The philosophy literature contains many criteria for emergence, often related to the mind–body problem (e.g., see Brandon 1990, 1996; Sober 1984, 1992, 1999; Wimsatt 2007; and Grantham's 2007 review), but these have been difficult to apply to clade dynamics. One simple operational approach is for a feature to be emergent at a given level if its evolutionary consequences do not depend on how the feature is generated at lower levels (Jablonski 2000, 2007; Jablonski & Hunt 2006). This approach is related to Brandon's (1990) application of the statistical concept of screening-off (where variation at the lower level is “screened off” from selection at the higher level) and to the multiple-realizability criterion for emergence (where a higher-level trait can be realized by many

Emergent traits:

species properties that are not reducible to organismic traits (e.g., geographic range size or population structure)

distinct combinations of lower-level properties); both are controversial in some situations but the general approach can provide a working hypothesis in the present context (see Brandon et al. 1994, Grantham 2007, Sober 1999, Sterelny & Griffiths 1999, Wimsatt 2007 for discussions). Thus, geographic range is a species-level property (see references in **Table 1**), not simply because most geographic ranges are determined by the overall distribution of conspecifics rather than by the movements of individual organisms, but because the macroevolutionary consequences—the positive relation between geographic range and extinction-resistance—tend to be similar regardless of how those ranges are mediated/attained at the organismal level (see below). Only geographic range size has been subjected empirically to this criterion, and so the effective hierarchical level of most others remains theoretical. However, only a few of the properties in **Table 1** need to be confirmed to open a large domain for strict-sense species selection: all species have a geographic range, a genetic population structure, and so on. What we really need to know is which traits are most likely to screen off, override, or significantly reinforce selection and other forces operating at other levels, and in what circumstances.

Cutting across the aggregate/emergent distinction is the separation of sorting processes into multilevel selection (MLS) 1 and 2 (a viewpoint developed by Arnold & Fristrup 1982 and Sober 1984 and formalized by Heisler & Damuth 1987; see also Damuth & Heisler 1988, Okasha 2006). In MLS1, the organisms are the focal level; changes in the frequency of organismic traits depend on selection both within and between larger units; that is, an individual's fitness depends in part on the phenotypes of other individuals in the population so that change in organismic properties both is affected by and will alter the larger units to which they belong. Most models for group selection (e.g., for the evolution of altruism) take this form (e.g., Damuth & Heisler 1988, Okasha 2006, Wilson & Wilson 2007), and I will discuss this no further, except to note that some researchers have applied the term group selection to selection on any unit above the organism level [e.g., Wright 1932, 1945 (as intergroup selection); Okasha 2003; Rice 2004; Van Valen 1975]. In contrast, for MLS2 the higher-level units such as species are the focal level, and the key variables are the origin and demise of those higher-level units, for example, speciation and extinction. The traits that influence speciation and extinction might reside at the organismic level (= effect-macroevo-lution) or at the species level (= strict-sense species selection).

Disputes over different senses of species selection are largely terminological and secondary to the broader theoretical implications of MLS: any higher-level sorting process irreducible to within-population evolutionary forces conforms to a hierarchical evolutionary theory. However, if we are to move from pattern to process, then the hierarchical level of the target of selection—that is, the nature of the interaction between the focal unit and its environment and not just the differential proliferation of species—is a key consideration.

Upward Causation: Effect-Macroevo-lution

Aggregate characters are expressed at the organismic level but may influence speciation and extinction rates and thus mediate effect-macroevo-lution, that is, differential origination and/or extinction owing to organismic traits. An impressive array of aggregate traits has been hypothesized or demonstrated to play such a role, from niche breadth to the intensity of sexual selection to clonality to propagule size (**Table 2**). Three striking features of this list, aside from its length, are as follows:

1. Many of these traits involve macroevolutionary trade-offs such that high origination rates are often expected to be accompanied by high species-extinction rates (e.g., Coyne & Orr 2004, p. 435; Gould & Eldredge 1977; Stanley 1979, 1990). For example, intense sexual

Table 1 Proposed species-level traits and their hypothesized impact on rates of origination (**O**) and/or extinction (**E**)

| Species-level trait (relative to another clade) | Impact on emergent fitness | References |
|--|---|---|
| Geographic range size | Low E and/or low O in widespread species | Brown 1995; Budd & Johnson 2001; Cheetham & Jackson 1996; Chown 1997; Cooper et al. 2008; Gaston 2003; Gould 2002, p. 657; Grantham 1995, 2001, 2007; Hansen 1980; Hunt et al. 2005; Jablonski 1987, 2000, 2007; Jablonski & Roy 2003; Koh et al. 2004; Levin 2006; Mayhew 2007; Meyer 2003; Okasha 2006; Purvis et al. 2000b; Reaka & Manning 1981, 1987; Rice 2004, p. 312; Roberts & Hawkins 1999; Rode & Lieberman 2004; Rosenfield 2002; Sterelny & Griffiths 1999, p. 206 |
| Patchiness of populations within range | Low E and low O with low patchiness | Owens et al. 1999, Roberts & Hawkins 1999 |
| Genetic population structure | Low E and low O with weak structure | Jablonski 1986; Rice 2004, p. 312; Roberts & Hawkins 1999; Vrba & Gould 1986, p. 224; intermediate metapopulation structure may confer low E , e.g., Gaggiotti & Hanski 2004 |
| Sex ratio | High E with biased sex ratio | Vrba 1989, Le Galliard et al. 2005 |
| Population size | Low E with large size, conflicting inferences for O | Boucot 1975; Budd & Johnson 2001; Mace & Kershaw 1997; McKinney 1997; Pimm et al. 1988; Vrba & Gould 1986, p. 219 |
| | Low E and high O with large population size | Levin 2006 (low E via broad geographic range, high O via large number of propagules) |
| Population density/local abundance | Low E and low O with high abundance | Budd & Johnson 2001; Gould 2002, p. 657; Meloro et al. 2007; Purvis et al. 2000b; Roberts & Hawkins 1999; Stanley 1986, 1990; some theoretical predictions involve low E and high O , e.g., Hubbell 2001 |
| Variability in population size | Low E with high variability | Pimm et al. 1988; Stanley 1986, 1990; Vucetich et al. 2000 (who reject Schoener & Spiller 1992 and other negative results); Inchausti & Halley 2003 |
| Intraspecific variation | Low E and low O with copious variation | Dobzhansky 1937; Eldredge 1985, p. 182; Lloyd 1988, pp. 110–112; Lloyd & Gould 1993 (“a good species-level trait that can be associated with genuine species-level fitness”); Okasha 2006, p. 203 |
| Mode of intraspecific competition | Low E with scramble competition (versus contest competition) | Best et al. 2007 |
| “Evolvability” or “versatility” | Low E and high O with high “evolvability” | Dawkins 1989; Gould 2002, pp. 1271–77; Lovette et al. 2002; Maynard Smith 1998; Mayhew (2007) considers this “an aggregate species-level trait”; see review by Pigliucci 2008 |
| Ontogenetic age structure | Little macroevolutionary study | Vrba 1989 |
| Social organization (breeding group size) | Low E and low O with large social groups | Vrba 1987, 1989 (with negative result); Muñoz-Durán 2002 |
| “Rate of variation production” (by mutation and recombination) | Little macroevolutionary study | Vrba 1989 |

Note that most traits exhibit the macroevolutionary trade-off discussed in the text so that these traits do not necessarily promote high species richness or net diversification (= emergent fitness = **O**–**E**). However, many empirical studies measure species richness without separating **O** and **E**. Species niche dimension or environmental breadth, usually treated as an aggregate trait, would be emergent if similar evolutionary effects obtain whether broad species niche is achieved by tolerant organisms or by intraspecific variation in ecological preferences.

Table 2 Proposed aggregate traits and their hypothesized impact on rates of origination (**O**) and/or extinction (**E**) (see caption to Table 1)

| Organismic-level trait (relative to another clade) | Impact on emergent fitness | References |
|--|--|--|
| Body size | Mixed—context-dependent? | Mixed empirical results [Jablonski 1996, McKinney 1997, Pimm et al. 1988 (varies with population size), Mayhew 2007, Purvis et al. 2000b. But large size is generally more vulnerable to anthropogenic extinction (Cardillo 2003, Purvis et al. 2005, Roberts & Hawkins 1999)] |
| Ecological specialization/ environmental tolerance (eurytopy versus stenotopy) (“niche dimension,” a species-level trait in Diniz-Filho et al. 2007) | Low E and low O in generalized or tolerant taxa, higher net diversification in some specialized taxa | Eldredge 1979; Vrba 1980, 1984, 1987, 1989; Jernvall & Wright 1998; Kammer et al. 1998; Purvis et al. 2000b; Roberts & Hawkins 1999 (mixed results); Bennett & Owens 2002; Harcourt et al. 2002; Juillard et al. 2003; Prendini 2001; Gage et al. 2002; Hernández Fernández & Vrba 2005; Mayhew 2007; but Phillimore et al. (2006) and Xiang et al. (2004) find high net diversification rate in generalized bird taxa |
| Competitive ability | Low E with high competitive ability | Roberts & Hawkins 1999 |
| Host specificity | Low E and low O in generalized taxa | Jaenike 1990, Price 1980; references in Mayhew 2007, but see Futuyma & Moreno 1988 |
| Intensity of sexual selection, sexual dimorphism, or sexual conflict (sometimes considered emergent trait) | Low E and low O with weak selection, Low E and low O where males dominate mate choice | Arnqvist et al. 2000; Barraclough et al. 1998, 1999; Misof 2002; Møller & Cuervo 1998; Owens et al. 1999; Partridge & Parker 1999; Prum 1997; Roberts & Hawkins 1999; Sampson 1999; Vamosi & Otto 2002 (in plants); Mank 2007; Mayhew 2007; Xiang et al. 2004; NOT Gage et al. 2002, whose results are challenged by Coyne & Orr 2004, p. 438; but also see Morrow & Fricke 2004, Morrow et al. 2003, Phillimore et al. 2006, and the mixed results of Ritchie’s 2007 survey |
| Asexual versus sexual reproduction | Low E and high O in sexual species | Barton & Charlesworth 1998; Burt 2000; Getz 2001; Holsinger 2000; Rice 2002; Stanley 1975b, 1979; and many more; but see Barraclough et al. 2003 |
| Semelparity versus iteroparity | Low E and low O in iteroparous species | Roberts & Hawkins 1999; also Ojeda et al. 2005, p. 163 (for analogous traits of sprouter versus nonsprouter life-histories in fire-recruiting woody plants; but see Bond & Midgley 2003) |
| Mating system | Low E in polygynous and polyandrous (versus monogamous) mating systems, although demographic stochasticity can be higher in polygynous systems (= high E ?) | Mitra et al. 1996; Legendre et al. 1999; Saether et al. 2004a,b (see also intensity of sexual selection, Table 1) |
| Allee effects (low population growth rate at small population sizes or densities) | Low E with weak allee effects (or low size threshold); O little-studied | Amarasekare 1998; Muñoz-Durán 2002; Reed 1999; Roberts & Hawkins 1999; Webb 2003; Dieckmann & Ferrière 2004; 10 examples in Holt et al. 2004, p. 254; Parvinen 2005 |
| Dispersal rates | Low E and low O with high dispersal | Jablonski 1986, Reed 1999, Roberts & Hawkins 1999, Xiang et al. 2004; but see Jablonski & Hunt 2006; Phillimore et al. (2006) find high net diversification rate in bird taxa with high annual dispersal |
| | Low E and high O with high dispersal | Levin 2006, Rosenzweig 1995 |

(Continued)

Table 2 (Continued)

| Organismic-level trait (relative to another clade) | Impact on emergent fitness | References |
|---|---|--|
| Generation time | Low E and low O with long generation time | Roberts & Hawkins 1999, Stebbins 1974; mixed empirical results (Marzluff & Dial 1991, Mayhew 2007, Purvis et al. 2000b) |
| Home range of individual | Low E with small home range, effects on O rarely considered | Purvis et al. 2000a,b, 2005 |
| Pollination mode | Low O with abiotic pollination, conflicting views on E | Coyne & Orr 2004, Dodd et al. 1999, Eriksson & Bremer 1992, Gorelick 2001, Kay et al. 2006, Waser 1998, Waser & Campbell 2004; but see Bolmgren et al. 2003; Ricklefs & Renner (1994) find that clades with both modes are most prolific |
| Floral symmetry | Low E and low O with radial symmetry | Sargent 2004 but not Kay et al. 2006 |
| Phenotypic plasticity | Mixed predictions: low E and low O , or low E and high O , with high plasticity | Agrawal 2001; Cavender-Bares & Wilczek 2003; Pigliucci 2001; Schlichting 2004; Sultan 1995; West-Eberhard 1989, 2003 (predicts low E and high O); van Alphen et al. 2004 |
| Eusocial insect caste polymorphism | Low E and low O with polymorphic workers (via tendency to single-queen colonies) | Hölldobler & Wilson 1990, Pamilo et al. 1997 |
| Colonial invertebrate polymorphism | Low E with polymorphic colonies | Anstey 1978, Hughes & Jackson 1990 |
| Trophic level | Low E and low O at low trophic levels | Roberts & Hawkins 1999, but see Jablonski 1995 |

selection evidently increases speciation rates in birds and insects but may also increase extinction rates by reducing effective population size and reducing viability owing to costly sexual characters; as it happens, the net result is generally diversification (e.g., Coyne & Orr 2004, p. 438). Taxa that break such covariation, locally in time and space or as a fixed aspect of their biology, may exhibit particularly extensive diversifications. Given the multiplicative growth inherent to clade diversification, even a modest shift of origination against extinction can have dramatic long-term effects. For example, small body sizes might increase sensitivity to geographic barriers and thus promote speciation even as accompanying large population sizes decrease species-extinction probability. For these and many other possible reasons, phytophagous insects are thought to combine relatively high speciation rates with low extinction rates (see Hunt et al. 2007, Labandeira & Sepkoski 1993, Mayhew 2007).

2. As just noted, the traits listed here can covary so that, for example, body size, population size, and generation time are loosely intercorrelated. On one hand, this covariation hinders the unequivocal recognition of key factors, but on the other hand it is probably telling us that simultaneous evaluation of variables will be a much more meaningful approach to understanding rate controls. The most extreme rates may prevail in clades combining multiple factors that all work in the same direction, with intermediate rates evident in clades that mix traits with opposing effects.
3. Inconsistent analytical results are recorded for several features. These discrepancies need not simply reflect different methods or sample sizes (although that is always a consideration), but

they could result from heterogeneous selective pressures. For example, bird species having small body sizes are at greater extinction risk when the predominant stress is habitat loss, whereas large-bodied bird species are at greater extinction risk when the predominant stress is predation (Bennett et al. 2005). Such conflicting outcomes deserve more systematic study (see also below).

Species-level heritability of most aggregate traits is relatively uncontroversial: If body size or ecological specialization is heritable at the organismic level, then those trait values might be expected to persist across most speciation events. The fact that many of the components incorporated into (positive) tests for ecological niche conservatism are organismic traits lends quantitative support to this intuition [Peterson et al. 1999, Wiens & Graham 2005; see also Freckleton et al.'s (2002) analysis of phylogenetic signal in a variety of traits and Smith et al. 2004 on body size]. However, this intuition might be violated in clades where ecological speciation is common, with new species arising as populations diverge ecologically (e.g., Dieckmann et al. 2004, Peterson et al. 1999, Schluter 2000, couch this contrast in terms of sympatric and peripatric speciation versus vicariant speciation). Species-level heritability of aggregate traits should be weaker or should become attenuated more rapidly over time for these groups so that the scope for consistent effect-macroevolution may vary among clades, speciation modes, and traits. On the other hand, the apparent conflict may be a matter of scale: much recent work on niche conservatism focuses on climatic niche dimensions, whereas ecological speciation involves habitat selection within limited areas.

This is not to say that every change in organismic phenotype must cascade upward to alter clade dynamics. One key attribute of a nested hierarchy is the asymmetry of effects: dynamics at lower levels need not be manifest at higher levels, although dynamics at higher levels must always propagate downward (e.g., Salthe 1985, Valentine & May 1996). A parasitic DNA sequence may never proliferate to the point of reducing the fitness of the host organism, and a virulent disease can devastate Caribbean *Diadema antillarum* subpopulations without exterminating the species or even significantly reducing its total genetic diversity. More generally, many selectively driven changes in organismal phenotype may have little effect on the mean extinction probability of the overall species or clade relative to a sister group. But extinguish the echinoid species, and by downward causation all the parasitic DNA sequences in its cells go with it. Decrease the extinction probability in a clade owing to the average geographic ranges of its species, and many organismic traits unrelated to biogeography can persist relative to those of a sister taxon.

Effect-macroevolution could reinforce rather than oppose the operation of selection at the organismic level, but as noted more generally above, it will be most clear-cut in cases of cross-level conflict. Such cases may be more widespread than generally appreciated and might include situations where selection favors organismic traits that tend to increase long-term extinction risk, for example, via reductions in geographic range size or population density. Sexual selection has been depicted in similar terms, where increased organismic fitness can increase species' vulnerability to extinction (e.g., Coyne & Orr 2004, p. 438). The most extreme cases, where organismic selection actually drives species into extinction, deterministically or by pushing them into states where stochastic extinction is inevitable, have been termed evolutionary suicide, Darwinian extinction, or self-extinction (Parvinen 2005, Rankin & López-Sepulcre 2005, Webb 2003). Darwinian extinction exists primarily in theory, but some empirical instances are known, both in the lab and in fisheries, where selection for smaller, faster maturing adults can produce individuals that have lower per-capita fecundities and are less effective at preying on enemies of juvenile conspecifics (Rankin & López-Sepulcre 2005 and references therein).

Species as Focal Level: Strict-Sense Species Selection

Strict-sense species selection poses a more difficult challenge, requiring the classic evolutionary triad of variation, interaction, and heritability (Lewontin 1970) to operate at the species level. Factors as various as geographic range size and patchiness, genetic population structure, sex ratio, and the “relative position of a species in the environmental space (e.g., its bioclimatic envelope)” (Diniz-Filho et al. 2007) have been proposed as emergent species-level traits for the interaction term (**Table 1**), but few have been evaluated critically. Fewer workers have addressed this problem, and many of these features are difficult to quantify rigorously in a macroevolutionary analysis. Nevertheless, some promising results are available, and it should be noted that the trade-offs seen for aggregate traits also occur here so that high origination rates are often thought to be accompanied by high extinction rates.

Geographic range has received by far the most attention as a factor for strict-sense species selection, and so I will discuss this feature in some detail. Range size certainly varies among species, and many analyses have found a positive relation between geographic range and extinction resistance (**Table 1**). The evolutionary consequences of broad or narrow geographic ranges tend to be similar regardless of how these ranges are mediated at the organismal level, suggested by the criteria noted above that it can be viewed as an emergent property at the species level. For example, widespread species of marine snails are geologically longer lived than restricted species, and the establishment and maintenance of these different ranges are statistically related, in part, to modes of larval development—an organismal trait—that differ in dispersal capabilities (Jablonski & Hunt 2006 and references therein). However, the range–duration relationship holds within gastropod larval types, among marine bivalves where range is not significantly related to larval mode, and among marine bryozoans, where range differences apparently derive mainly from rafting of adults (Cheetham & Jackson 1996). Differential species survival evidently depends on the emergent, species-level property, that is, the scale of the species’ range, and not directly upon any single underlying organismal trait (suggesting screening-off of those traits by range). In another instance of the macroevolutionary trade-off discussed above, speciation rates also appear to be inversely related to species’ geographic range, although some theories would suggest that the opposite and the generality of the empirical pattern needs further testing (Jablonski & Roy 2003; see also Gaston 2003; Lester & Ruttenberg 2005; Meyer 2003; Reaka & Manning 1981, 1987). The argument is that the many factors that interact to confer broad geographic range, such as strong dispersal ability and wide environmental tolerances, also tend to damp speciation probabilities in many groups—a species-level example of the macroevolutionary trade-off mentioned above.

Finally, geographic range appears to be heritable at the species level, in the sense that closely related species tend to attain range sizes that are more similar than expected by chance (Beck et al. 2006, Blackburn et al. 2004, Brown 1995, Hunt et al. 2005, Jablonski 1987, Jablonski & Hunt 2006, Jones et al. 2005, Qian & Ricklefs 2004, Ricklefs & Latham 1992, Waldron 2007; several of these researchers address the analytical concerns raised by Webb & Gaston 2003, 2005; and Hunt et al. 2005 provide a more robust method that effectively reverses Webb & Gaston’s 2003 results). Results from extant species’ ranges tend to be weaker than the paleontological ones, and this is not surprising: species show a variety of range-size dynamics over their histories (e.g., Foote et al. 2007, Gaston 2003, Jones et al. 2005, Liow & Stenseth 2007). Today’s narrow-ranging species could be in an early expansion stage, at a stable maximum range, or in decline, so that an analysis of present-day species is analogous to a traditional heritability study that fails to standardize by ontogenetic age. By contrast, paleontological analyses can incorporate maximum observed range, which also partly helps to compensate for sampling effects.

Directional speciation: a bias in the direction of phenotypes produced in a succession of speciation events

Just as the heritability of organismic traits can evolve and can vary according to environmental context, the heritability of range-size and other species-level traits might be expected to evolve within and among clades. As Rice (2004, p. 316) notes, one way that organismic selection reduces the efficacy of species selection is by reducing species-level heritability. This possibility has not been explored theoretically or empirically at the species level.

Several researchers equate organismic death and species extinction to the extent of ruling out extinction as a component of emergent fitness. For example, Cracraft (1990, p. 40, *his italics*) says “species, *as cohesive entities or units*, do not become extinct. Species extinction is a cumulative effect of the death of individual organisms” (see also Gould & Eldredge 1977, Vrba & d Eldredge 1984; Sterelny 2001, p. 123; Grantham 1995, p. 310 is less absolute). True, species—discrete genealogical units within larger clades—become extinct when the last organism dies. Factors such as disease, predation, or physiologically intolerable environmental change where spatial displacement is not an option can cause the piecemeal extermination of every organism within a gene pool. However, as Lloyd (1988, p. 110) says, “The focus on individual death in the case of extinction is a mistake.” If we are interested in the demography of clades—the statistics of their origin, expansion, contraction, and extinction—then it is easy to see that species-level characters can influence the relative extinction probabilities of species and that organismic traits can actually increase that extinction probability even if favored at the organismic level.

Directional Speciation and Species Drift

By analogy with mutation bias at the organismic level, directional speciation has been invoked as an alternative to species sorting in the generation of macroevolutionary trends (see Hallam 1978, 1998, Stanley 1979). Such directional speciation might result, for example, from developmental factors that bias the probability of phenotypic change in particular directions, giving rise to “genetic lines of least resistance” (Schluter 1996, 2000). In perhaps the best-documented case, the deep-sea ostracod *Poseidonamicus* shows little evidence for gradual within-species evolution, but both speciation events and stepped anagenetic transformations are biased in the direction of higher phenotypic variance in probable ancestors (Hunt 2007a). Alternatively, Grant’s (1963, 1989) speciation trends involve undirected speciation that gives rise to a directional chain of speciation events, owing to competition and ecological opportunity. Unfortunately, highly asymmetrical, comblike evolutionary trees can also be generated by extinction (e.g., Heard & Mooers 2002) so that tree topology alone is not diagnostic of directional speciation (see Maddison 2006).

Evolutionary trends shaped by directional speciation are sometimes termed driven trends and treated as a subset of active trends, which also include trends shaped by differential origination or persistence of species that arise randomly relative to the overall trend (= broad-sense species selection). These active processes are contrasted with passive trends, created by simple diffusion over time, which can shift the maximum or minimum values of a character away from its initial value, particularly given a boundary constraint such as a minimum viable body size for the clade (see Alroy 2000; McShea 1994, 1998, 2000; Wagner 1996; Wang 2001 for discussion and varying terminology). Despite numerous case studies, the insights stemming from Stanley’s (1973) observation that apparent trends can arise by passive diffusion still have not been fully assimilated into work on large-scale diversification patterns.

Stanley (1979, pp. 195–96) proposed selection among demes rather than individuals as the source of trends produced by directional speciation: if the morphologically most extreme demes (specifically, peripheral isolates in his model) preferentially give rise to new species, then demic, or isolate, selection can drive a trend over multiple species [Gould (2002, p. 702) reinvents this

idea; for an early version of this approach, see Boorman & Levitt (1973), who analyze interdemec selection among peripheral isolates, a case of MLS2 below the species level]. This mechanism has not been tested empirically and may be problematic for paleontological data by postulating the existence of populations too transient to be reliably detected in the fossil record. However, combined neontological–paleontological analyses of modern populations at the tip of a well-documented evolutionary trend could provide valuable insights.

Upward and downward causation can occur without any active process. At any hierarchical level, drift can be viewed as differential reproduction owing to chance rather than interaction at the focal level, and such drift will of course affect the frequencies of lower level entities. The effects of drift can also propagate upward, of course, by driving alleles to fixation, phenotypic characters to oblivion, or demes and species to extinction. A rich literature exists on drift at the genic level, but stochastic processes at higher levels have received little formal attention except as null models (e.g., Raup 1981, Raup & Gould 1974, Wollenberg et al. 1996). Nevertheless, such phylogenetic drift (Stanley 1979, pp. 183–84; species drift of Gould 2002, p. 736; Levinton et al. 1986) could in principle change the amount and nature of variation available for selection at multiple levels, just as the more familiar drift within populations can shift genotype frequencies. In fact, the small number of species contained in most clades at any one time suggests that drift will often be a more potent force at that level than at the level of bodies within populations (Gould 2002, pp. 736, 893). Drift at one level can be deterministic at another, of course: selection operating in different directions in different populations among many species can result in stochastic dynamics for clades, for example (e.g., Gould 2002, Raup 1981, Raup & Gould 1974).

TOWARD A FORMALIZATION OF SPECIES SELECTION

Far less work has been devoted to developing a formal theory of species selection than to group selection. One failing in the work that has been done, my own included, is a tendency to focus on situations where higher level processes are so strong that analyses at that level alone are sufficient to build the argument. But if sorting processes are operating at all levels simultaneously, and upward and downward causation is pervasive, then the long-term evolutionary behavior of a clade in morphospace, or the waxing and waning of its species richness, will not coincide exactly with selective pressures at any single level because it is the resultant of forces operating at multiple levels. Further, many approaches suffer from a bottom-up formulation, where only the selection that cannot be explained by the lower level is attributable to higher level processes. Because these approaches are generally verbal rather than mathematical, or at best focus solely on blatantly opposing forces across levels, they cannot begin to detect concordant sorting processes at multiple levels (as when organismic selection favors a group that also has a population structure promoting high speciation rates).

A fully operational approach to quantifying sorting processes among multiple levels has yet to appear. Clearly, such an approach should partition MLS into contributions of processes at different levels, analogous to the Price equation, contextual analysis, and other models developed by students of the MLS1 category of group selection. Although there is much room for novel approaches, for example, by formulating rival likelihood models, such work has barely begun. I briefly review methods that have been proposed. Note that the first two of these models are chiefly conceptual, designed to ask when species selection can supersede organismic selection in assembling complex adaptations. The domain of species selection is now seen as mainly involving the persistence and among-clade frequencies of such adaptations (despite Rice's 1995 provocative approach), and from that standpoint the second two models are empirically more tractable and mechanistically more realistic. As Raup (1994) emphasized, however, this sorting process might also be crucial in

preserving, multiplying, or removing intermediates, whenever complex adaptations require more time to assemble than is available over the duration of a single species (e.g., the terrestrialization of plants, vertebrates, and arthropods), although this idea has not been evaluated rigorously.

Diffusion Model

One of the first formal approaches to species selection was Slatkin's (1981) diffusion model, which modeled the evolution of a continuous phenotypic character in terms of diffusion subject to the combined effects of phyletic evolution, speciation, and extinction. The model has not been applied since (although see Foote 1996), perhaps because it requires assumptions on the trait heritability, effective population size, and generation time of the target species. This is not for the faint of heart (what was the N_e of a fossil scallop that ranged 5000 km from New Jersey to Texas, or a circum-equatorial planktic foraminiferan?), although combinations of plausible values could probably be explored. The simple diffusion assumption also ignores fluctuations in phenotype space "critical to generating realistic patterns of morphospace occupation" (Pie & Weitz 2005), and so may be difficult to apply to relatively small clades.

Genetical Model

Rice's (1995, 2004) genetical model for species selection also evaluates the efficacy of species selection relative to organismic selection in changing phenotypes. Here the key parameters are speciation rate per generation, the mutation rate of the character, selection coefficients, and the initial population size of a new formed species. Again these parameters will be difficult to quantify for most extinct populations, but they do predict that clades combining high speciation rates, long generation times, and moderate mutation rates (10^{-6} per generation) will be more subject to species selection as a force that can overwhelm organismic selection. This prediction has not been evaluated by among-clade comparisons.

General Linear Models

General linear models (GLMs), including both simple and multiple regressions, have increasingly been used to assess the relative roles of different biological attributes in determining speciation, extinction, and diversification rates. If species-level and organismic traits are defined a priori, their relative contributions can be assessed in a manner that can separate strict-sense species selection from effect-macroevolution. For example, geographic range (a species-level trait) significantly predicted species duration in marine mollusks when analyzed separately and jointly with larval mode (an organismic trait sometimes linked to range as discussed above). Adding geographic range to models containing only larval mode significantly increased model fits, indicating that geographic range was not redundant with larval mode in predicting species survivorship, whereas adding larval mode to models containing geographic range provided only marginal and insignificant improvement in model fit (Jablonski & Hunt 2006). Similarly, multiple regression models found geographic range to be a highly significant predictor of extinction risk in Carnivora, whereas several organismic traits including body mass and age at sexual maturity were not (Purvis et al. 2000a, 2005a). Likelihood methods may offer another approach, particularly if extended to continuous variables (Maddison et al. 2007). These statistical methods obviously cannot themselves partition features between emergent and aggregate categories, but they have the benefit of measuring the relative contributions of factors rather than requiring opposing selective forces across levels before processes can be evaluated.

The Price Equation

Price's (1972) equation expresses the change in phenotype between parent and offspring generations in terms of the covariances between fitness and phenotype both within and between groups (broadly defined), and thus has considerable potential for examining MLS (Arnold & Frisrup 1982; Damuth & Heisler 1988; Frank 1995, 1997, 1998; Gould 2002; Heisler & Damuth 1987; Lloyd 1988; Okasha 2006; Rice 2004; Sober & Wilson 1998). Some caution is needed, because the Price equation can mislead in certain cases of MLS1, if group selection is evaluated by equating the mean fitness of group members with group fitness (see Okasha 2006, Sober 1984, van Veelen 2005; an alternative approach, contextual analysis, also applies only to MLS1; see Heisler & Damuth 1987, Okasha 2006, Rice 2004). The Price equation partitions the effects of selection among levels using covariance, which is a weak tool for detecting causal relationships (cf. Rice 2004, p. 324); GLMs (as above), though also imperfect, focus more closely on relationships that are not simply a consequence of shared correlations. Operationally, however, the two approaches can converge, and the conceptual power of the Price approach is promising.

Application of a hierarchically expanded Price equation to species selection was suggested by Arnold & Frisrup (1982; see also Gould 2002, Lloyd 1988, Lloyd & Gould 1993), and an empirical analysis was finally provided by Simpson (2006, 2008), who quantified the relative contributions of (broad-sense) species selection and directional speciation (which he attributed to organismic selection) in the evolutionary simplification of calyx structure in Paleozoic camerate crinoids. Essentially this amounted to combining a regression of diversification rate against calyx complexity (essentially an emergent fitness surface, by analogy to microevolutionary fitness surfaces) with an assessment of the contribution of directional speciation, achieved by quantifying the skew of the complexity–frequency distribution (cf. McShea 1994). This approach detected and quantified both processes, even though they were operating in the same direction. Such an escape from the usual, highly limiting search for opposing forces at different levels is a significant step forward.

Evolutionary stasis:
bounded
nondirectional
phenotypic change
during the history of a
species

THREE OVERSIMPLIFICATIONS TO AVOID

Punctuated Equilibrium as a Prerequisite for Species Selection

Proponents of species selection were spurred by the realization that many species follow a punctuational dynamic in the fossil record, exhibiting evolutionary stasis through much of their histories (for recent overviews, see Eldredge et al. 2005, Hunt 2007b, Jablonski 2000, Jackson & Cheetham 1999). Net phenotypic changes in clades where stasis or nondirectionality predominates should thus involve a significant contribution from species sorting and/or directional speciation (Eldredge & Gould 1972; Gould 1982, 2002; Gould & Eldredge 1977; Stanley 1975a, 1979). This is a legitimate argument, but species-sorting processes can also operate in gradually evolving lineages. The relative contributions of among-species sorting and intraspecific gradualism depends on the extent of variation generated by cladogenesis and anagenesis, and on the covariation of origination and extinction rate with phenotype (Arnold & Frisrup 1982, Bookstein et al. 1978, Slatkin 1981; see also Okasha 2006 and Rice 1995, 2004). Systematic analyses are needed, but the literature is rich in situations where the gradual, intraspecific components of large-scale trends prove ineffective in predicting the net phenotypic displacement of the clade. For example, the macroevolutionary trend toward size increase in Gingerich's (1976) classic *Hyopsodus* data derives not from intraspecific size increase, but from a higher level dynamic containing three gradual size increases, one punctuational size increase, one period of size stasis, and three gradual size decreases (Bookstein et al. 1978, p. 133). This does not mean that organismal selection was not involved in the evolutionary changes, of course, but it undermines simple extrapolation of short-term processes to geologic

timescales as a complete explanation even for clades containing anagenetic segments. At the same time, it shows that the punctuational mode is not a prerequisite for species selection (as Slatkin 1981 recognized, *contra* Gould 2002).

Intrinsic Rates as Wholly Divorced from Extrinsic Factors (Physical and Biotic)

If only on operational grounds, analyses of species sorting have focused on intrinsic biotic traits. As already mentioned, however, the impact of a given trait on evolutionary dynamics may change with extrinsic pressures (e.g., Bennett et al. 2005, Fréville et al. 2007, Purvis et al. 2000b). Further, the efficacy or even the sign of its evolutionary effect can vary in time and space. For example, geographic range at the species level is important to molluscan clade survivorship both before and after but not during the end-Cretaceous mass extinction (Jablonski 2005). Long-term changes in the biotic environment can also alter the association between trait values and extinction/origination probabilities, as apparently occurred with the increase of predation pressure in marine communities (e.g., Jablonski 2008a, Stanley 1986, 2008). Large-scale spatial variations in evolutionary dynamics have also been recorded, most notably along latitudinal gradients (e.g., Hawkins et al. 2007, Jablonski et al. 2006, Mittelbach et al. 2007). All of these factors mean that comparative studies must be interpreted carefully: even sister-group analyses may incorporate one or more of these extrinsic factors. More work explicitly designed to test intrinsic and extrinsic factors and their interaction over time is needed.

Intrinsic Factors as Fully Independent Variables

As noted above, most analyses of links between intrinsic biotic factors and evolutionary dynamics have been univariate. Although this strategy has provided valuable insights, it is clearly an oversimplification: traits covary for good ecological and evolutionary reasons, and independent factors can reinforce or cancel each other out. Multivariate treatments are needed and becoming increasingly available (e.g., Fréville et al. 2007; Harnik 2007; Purvis et al. 2000a, 2005a; Jablonski 2008b; Jones et al. 2005; Phillimore et al. 2006). The challenge is to fit these analyses into a common framework (and to revisit the many univariate studies in **Tables 1** and **2**), facilitating broader conclusions on the nature of these interactions and their evolutionary consequences.

PALEONTOLOGICAL AND NEONTOLOGICAL DATA

The strengths and weaknesses of data from living and fossil systems have been widely discussed (see Jablonski 2008a for a recent discussion). Besides sampling uncertainties that inevitably accompany an incomplete fossil record (see Foote & Miller 2007 for an introduction to statistical approaches to such problems), paleontological data can access only a few aspects of the organisms' phenotypes, and genetic analyses are unavailable for all but the youngest material. One clear result from the explosion of molecular phylogeographic analysis is that many named species include multiple reproductively isolated, biological species (e.g., Bickford et al. 2007). This important finding need not be a major problem for paleontological analysis of clade dynamics for at least two reasons. First, rigorous morphometrics often detect morphospecies that correspond quite closely to genetically defined biospecies (e.g., Jackson & Cheetham 1990, and 15 other references in Jablonski 2000). Second, comparisons of relative speciation or extinction rates and species durations will be misleading only if apparently species-poor groups preferentially contain the largest numbers of cryptic species; if the numbers are random, uniform, or lower in the species-poor groups, then comparative analyses will be robust. In the most extensive synthesis to date, Pfenninger & Schwenk

(2007) found cryptic species to be homogeneously distributed among higher animal taxa, although greater phylogenetic resolution would be valuable here. For marine mollusks, which constitute many of the fossil clades analyzed for species, the scattered literature suggests that the clades rich in morphospecies also tend to contain the greatest numbers of biospecies (Jablonski 2000), presumably because both the numbers are related to levels of gene flow and genetic fragmentation. Thus, errors in estimating species numbers will tend to be conservative for many research designs.

Neontological data provide a much wider range of traits for analysis than do fossil data and are rich in patterns that may have arisen by species sorting. The extensive literature on phylogenetically independent contrasts (e.g., Freckleton et al. 2002) can be seen in this light, documenting differential proliferation among clades owing to the distribution of intrinsic biotic properties (Coyne & Orr 2004; Jablonski 2000, 2007). The same could be said for the rather more problematic literature on key innovations (e.g., Ree 2005). Many of these analyses necessarily measure net diversification—interclade differences in species richness—without decomposing dynamics into origination and extinction components. Thus causal mechanisms are often unclear, and additional factors can enter into diversity relationships, as when narrow niches promote regional coexistence of species rather than increased speciation rates. Methods are available for estimating speciation and extinction rates from phylogenies of extant species, but in many instances assumptions are strong and uncertainties large, presenting, as Ricklefs (2007) notes, formidable challenges. Even less explored from this standpoint is the macroecology literature. Its analyses of the relationships among organismic traits and species' spatial distributions (e.g., Brown 1995, Gaston 2003, Gaston & Blackburn 2000) provides many potential instances of upward causation from the organismic level, and downward causation via differential production and survival of species according to their geographic ranges (see Cooper et al. 2008). The same potential holds for conservation biology: given that geographic range is one of the strongest predictors of extinction risk, today's biota appears to be in the midst of massive experiment in strict-sense species selection. Human-driven effect-macroevo- lution is also being imposed by activities such as strong size-selective harvesting of marine and terrestrial animals (e.g., Fenberg & Roy 2008). Integrated paleontological and neontological analyses, starting with present-day species and analyzing the preceding dynamics through a rich fossil record, would be a powerful way forward.

SUMMARY POINTS

1. Differential speciation and extinction have been increasingly recognized as processes that can shape phenotypic differences among clades, with effects cascading upward and downward across levels. Such differences in emergent fitness may generally be unlikely to assemble complex adaptations but may be important in determining the frequency of such adaptations, their distributions across phylogenies, and the persistence, proliferation, or termination of intermediate stages available to organismic selection.
2. Species sorting (= broad-sense species selection) comprises (*a*) effect-macroevo- lution, where organism-level traits (aggregate traits) affect speciation and extinction rates, and (*b*) strict-sense species selection, where species-level traits affect speciation and extinction rates. **Tables 1** and **2** list features proposed to fall under each category and empirical data supporting their efficacy.
3. Species selection need not oppose organismic selection to be an important evolutionary force, nor does it require punctuated equilibria (with species being static over much of their histories) to operate.

4. Hierarchical approaches to evolution tend to focus on intrinsic biotic traits, but these traits interact and so should not be treated as independent variables, and they cannot be fully divorced from extrinsic physical and biotic factors.
5. Of potential species-level properties, only geographic range has received serious analysis: in at least some instances, it shows the requisite variation, association with differential speciation and extinction, and heritability to affect evolutionary dynamics via strict-sense species selection.
6. Neontological results from phylogenetic comparative analyses, macroecology, and conservation biology strongly suggest that broad-sense species selection is pervasive, and they provide rich opportunities for collaborations with paleontology.

FUTURE DIRECTIONS

1. The relative frequency and impact of effect-macroevo-lution, strict-sense species selection, and directional speciation as an alternative to the first two, are empirical questions that require a much larger database for resolution.
2. Several formalizations of species selection have been proposed, but none is fully satisfactory. Hierarchical expansion of the Price equation seems a promising approach, but worked examples are needed across a range of situations.
3. Clades often exhibit a macroevolutionary trade-off wherein traits that confer, for example, high origination rates also impose, directly or by correlation with other traits, high extinction rates. These trade-offs, and the factors that evidently relax or break them to permit clades to expand dramatically, need to be better understood.
4. The strength and evolution of heritability for both aggregate and species-level traits are poorly understood, but such heritability is a crucial to long-term evolutionary dynamics.
5. Most importantly, new approaches and empirical research programs integrating the rich phenotypic and genetic data of neontology with the detailed temporal and spatial dynamics available to paleontology should be a high priority. This is of more than theoretical interest, because anthropogenic stresses on the modern biota are imposing massive experiments in strict-sense species selection and effect-macroevo-lution.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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