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Evolvability

A Unifying Concept in Evolutionary Biology?

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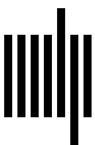
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17 **Evolvability and Macroevolution**

David Jablonski

Evaluating evolvability from a multilevel, macroevolutionary perspective is difficult, and integration of paleobiological and neontological data is essential for a deeper understanding. The operational approach proposed here tests for among-clade differences in phenotypic diversification in response to an opportunity, such as that encountered after a mass extinction, entering a new adaptive zone, or entering a new geographic area. By analyzing the dynamics of clades under similar environmental conditions, the aim is to approximate a macroevolutionary common-garden experiment that factors out shared external drivers to recognize intrinsic differences in evolvability. Diversity-disparity plots can track clades to determine when their phenotypic productivity exceeds stochastic expectation from their taxonomic diversification. Factors that evidently can promote evolvability include modularity (albeit contingent on alignment of selection with modular structure or with morphological integration), pronounced ontogenetic changes in morphology, genome size, and a variety of evolutionary novelties, which might be evaluated using macroevolutionary lags and dead-clade-walking patterns. High speciation rates may indirectly foster phenotypic evolvability. Although mechanisms are controversial, clade evolvability may be higher in the Cambrian, and possibly early in the history of clades at other times; in the tropics; and, for marine organisms, in shallow-water disturbed habitats. An expanded version of this chapter has been published in the journal *Evolutionary Biology* (Jablonski 2022).

17.1 Introduction

As Jane Austen might have said with a little biological training, it is a truth universally acknowledged that not all traits, populations, species, or clades have been equally labile or productive over their evolutionary lifetimes. A fundamental challenge in addressing such contrasts lies in distinguishing the role of intrinsic factors at various levels (from the configuration of gene-regulatory networks in an organism to the geographic extent of a clade) and extrinsic factors (from local competition to global climatic upheavals) in determining such differences. (See Jablonski 2017a,b for a general discussion of intrinsic and extrinsic factors in macroevolution, i.e., evolution above the species level.)

One potential intrinsic factor is evolvability. Evolvability has been defined in many ways (see Brown 2014; Nuño de la Rosa, chapter 2),¹ but when treated in general terms—the disposition or propensity to evolve, often referring specifically to adaptive evolution—

1. References to chapter numbers in the text are to chapters in this volume.

it can reside at any level within the biological hierarchy. In the macroevolutionary perspective adopted here, the focus will be on species (i.e., reproductively isolated, genealogical units) and clades (i.e., sets of species that comprise all, and only, descendants of a single ancestral species). To understand macroevolutionary dynamics, we need to determine whether species and clades differ in their intrinsic evolvability, and if so, why—and whether those differences are stable over a clade's history. Conversely, we need to determine whether the genetic and developmental mechanisms thought to promote evolvability in the short term have predictable long-term, large-scale evolutionary consequences. This is a challenging agenda, because inferences at the requisite scale and hierarchical level almost always rely on indirect evidence. This chapter cannot provide definitive answers, but in it, I attempt to outline macroevolutionary approaches to evolvability, first among clades regarding intrinsic traits that may promote or reduce evolvability, and then addressing variation in evolvability across time and space. The aim is to present an operational macroevolutionary approach, and to organize questions and potential examples to stimulate further theoretical and empirical research.

17.2 Operationalizing Evolvability in a Historical Context: Testing Macroevolutionary Hypotheses

The term *evolvability* might apply to any macroevolutionary currency, such as taxonomic diversity, functional variety, or morphological disparity; indeed, a long-standing question has been the degree of covariation among those currencies in different situations (Jablonski 2017a,b; Folk et al. 2019; Martin and Richards 2019; Shi et al. 2021). I propose to confine *evolvability* in macroevolution to phenotypes, with the hypothesis that evolvability is manifested in the behavior of traits and clades in a quantitative morphospace or functional space. An enormous literature exists on factors that promote or damp speciation and taxonomic diversification, but the propensity to achieve reproductive isolation, or to accrue taxonomic richness, probably involves a very different set of organismal and species-level attributes from those promoting the evolvability of form or function (Jablonski 2017b). Thus, expanding evolvability to include taxonomic rates or patterns in terms of evolvability probably is not useful.

One way to operationalize evolvability in macroevolution is as the differential (phenotypic) ability to take advantage of, or respond to, opportunity. This comparative approach is broadly analogous to the measurement of evolvability in terms of differential responses of traits to a unit strength of directional selection (Hansen and Pélabon 2021). Both intrinsic and extrinsic factors can create the opportunities—the acquisition of a novel structure, developmental pathway, or mode of life; entry into a novel ecosystem by surviving a mass extinction, invading a new landmass, or encountering newly evolved or introduced resources—and the analysis entails comparison of how clades performed in response (for useful discussions of evolutionary opportunity, see Losos 2010 and Gillespie et al. 2020). The difficulty for macroevolutionary analysis, of course, is that no two convergent evolutionary novelties are truly identical, and no two clades are likely to experience an environment in identical ways. However, because we can set prior expectations for the consequences of at least some confounding

factors, we can frame hypotheses incorporating them that can be tested in a meaningful way. The aim is to frame a macroevolutionary equivalent of a common-garden experiment, analyzing the behavior of clades under shared or similar circumstances.

This phenotypic approach, predicated on *net* phenotypic shifts or gains of disparity in morphology or function, also differs from a view of evolvability as a capacity for a species or clade to realize variation in any direction from a starting phenotype (Brown 2014; i.e., minimal developmental bias; see Uller et al. 2018). The “bias” approach would allow clades to be evaluated in isolation and perhaps may be useful over short timescales, but it is insufficient for macroevolutionary purposes. Many clades traced through multivariate morphospaces (“*phyломорфосpaces*”) undergo much movement in morphospace with little net expansion or shift compared to related clades; see, for example, the contrasting echinoid clades in figure 17.1. Similarly, frequent changes in discrete characters, even if apparently isotropic around a given starting point, need not yield extensive net change when homoplasy is common across the phylogeny, so that clades undergo many state changes but capture few of the new states (see Foote 1997; P. Wagner 2000; Oyston et al. 2015). This is one reason for heterogenous results on the correlation between (morpho)speciation rates and overall phenotypic evolution: Much total change can occur while repeatedly traversing a limited range of morphologies. The larger question remains: whether or how often among-clade differences in apparent evolvability can be understood, and predicted, in terms of intrinsic differences rather than simply reflecting the operation of extrinsic pressures. Of course, the intrinsic-extrinsic distinction is not clearly demarcated, and both factors operate in concert to some degree; but the abovementioned macroevolutionary common-garden approach can help tease apart intrinsic among-clade differences.

The two major arenas for macroevolutionary analysis—the fossil record and comparative data on extant taxa—are essentially historical or retrospective, each with strengths and weaknesses; they are most powerful when applied in concert, although integrating them is difficult (among many others, see, e.g., Quental and Marshall 2010; Jablonski 2017b; Mitchell et al. 2019). Neontological approaches (mostly) begin with genetic or developmental data thought to indicate evolvability and attempt to recognize how they have shaped the large-scale dynamics of the clade leading to the present day; paleontological analyses (mostly) begin with the phenotypic dynamics and attempt to exclude confounding factors to recognize differences in intrinsic evolvability among clades. In either domain, the first step is to frame *comparative* analyses, potentially identifying the role of intrinsic biological properties relative to the myriad extrinsic factors that can drive differences in evolutionary tempo and mode among clades in time and space.

17.2.1 Observations on Extant Organisms

As noted, one approach measures attributes in extant populations that might impose or reflect differing degrees of evolvability of traits or clades, and then tests predictions retrospectively (i.e., by analyzing macroevolutionary outcomes or estimated dynamics of those traits or clades). Some intriguing analyses have done just that (e.g., Goswami and Polly 2010 on primates versus carnivores [with important later work incorporating extensive fossil data]; Haber 2016 on ruminants; Houle et al. 2017 on *Drosophila*). Such analyses require some strong or poorly understood assumptions. These include:

- The stability of G-matrices that capture aspects of the genotype-phenotype map, and thus the utility of extrapolating from present-day data (see Hansen and Pélabon 2021; Hansen, chapter 5; Pavličev et al, chapter 8), and their roles in determining properties, such as the distribution of accessible phenotypes around a given starting point, at these scales, with a variety of empirical outcomes; further analyses in a multispecies phylogenetic framework would be valuable, with an urgent need for new genetic and developmental model systems that have robust fossil records (see Love et al. 2022; Voje et al., chapter 14).
- The robustness of taxonomic or morphological dynamics derived from the topology of large molecular phylogenies. Some progress has been made here, but separating speciation and extinction rates from net diversification—potentially important for testing hypotheses of cause and effect in morphospace occupation (as in Huang et al. 2015) remains challenging (e.g., Louca and Pennell 2020; Love et al. 2022), as does the problem of inferring ancestral character states from extant taxa alone (Slater et al. 2012; Betancur-R et al. 2015; Marshall 2017); and more generally, evolutionary modeling is demonstrably improved and results shift when fossils are incorporated (Mongiardino Koch 2021, citing twelve studies).
- The focal clade is today at its maximum morphological breadth; this is a generally unstated assumption required for phylogenies containing only extant species, but it is patently false for many clades having a reasonable fossil record, from oysters to cephalopods to elephants to horses to hominins. The extinct forms are often not simply extensions along existing morphogenetic lines but variations that might seem highly improbable, given today's representatives, for example, giant ground sloths (terrestrial *and* aquatic), rainforest-dwelling carnivorous kangaroos, sharks with coiled tooth arrays, uncoiled or spiny nautiloids, and sea urchins with periscope-like extensions (see Jablonski 2020 for references; even the quintessential static lineage, the horseshoe crabs, has exhibited bursts of phenotypic diversification that pushed beyond their current limited repertoire—see Bicknell et al. 2022).

17.2.2 Observations in the Fossil Record

Paleontological analyses pertaining to evolvability are beset by a different set of strong assumptions. Sampling and preservation can distort or even generate apparent patterns, although increased understanding of such potential biases have reduced their impact. Only post-embryonic, phenotypic data are available for most extinct taxa, and so the developmental and genetic underpinnings of observed contrasts must be inferred. Particularly challenging is the assessment of negative evidence (also an issue for neontological data, of course), and of the role of intrinsic and extrinsic factors in determining vacancies or boundaries of a clade's morphospace. Some vacancies are longstanding and phylogenetically localized, and thus may represent a lack of developmental capacity, at least for the clades presented with these opportunities (Vermeij 2015; Jablonski 2020). Others may reflect extinction and insufficient time to re-occupy vacated morphospace (consider mammalian body sizes in the Americas, although humans have surely now blocked that evolutionary route). Furthermore, morphospace occupation can be limited by preemptive occupation or later, displacive conquest of portions of the space by competing clades. Displacive competition seems to be scarce at macroevolutionary scales, but preemptive, incumbency patterns or priority effects seem relatively common (see Jablonski 2008a, 2017b; Benton 2009; Tilman and Tilman 2020; and Tomiya and Miller 2021 for a study

that may find both effects). Other negative interactions, such as predation and parasitism, can promote or impede phenotypic or taxonomic diversification, as can positive interactions such as mutualism, and either type can sometimes increase extinction probabilities (see Vermeij 1987; Jablonski 2008b; Hembry and Weber 2020). Comparative analyses of clades presented with similar opportunities can control for some of these uncertainties, and temporal and spatial paleo-data can be especially valuable, with insight not just into extinct phenotypes demonstrably accessible to a clade but lacking today, but also into potential interactions: clades cannot impede one another if they did not co-occur.

Despite these drawbacks and complications, many analyses do suggest among-clade and temporal differences in evolvability, with macroevolutionary consequences. Some of these are discussed in the following sections.

17.3 Features Enhancing Evolvability of Clades

17.3.1 Modularity

The developmental property most often proposed as associated with evolvability is modularity. The general view has been that greater modularity enhances evolvability (e.g., Wagner and Altenberg 1996; Love et al. 2022; Vermeij 1974, 2015 as “versatility,” which he associates with modularity in the later paper). However, many different types of modules are recognized, including functional, developmental, genetic, and evolutionary modules (see the references in Jablonski 2017a), and we lack clarity on how they are related, with mixed results on the positive, negative, or negligible relation between the strength of modularity and macroevolution (Rhoda et al. 2021 and references therein). For modularity to enhance evolvability, the intrinsic structure of modules—that is, genetic or developmental modules—must be configured along viable lines, which may or may not be the case (e.g., Pavličev and Hansen 2011; Pavličev et al., chapter 8), and align with internal selection (the need for body parts to function together) and external selection by the environment. Otherwise the covariation of traits within modules can instead impede evolution. In principle, the covariation structure imposed by morphological integration—not strictly the antithesis of modularity but useful in this context—can enable more rapid and extensive evolutionary change in certain directions than would emerge from strictly isotropic or unbiased variation (Goswami et al. 2014; Felice et al. 2018; Uller et al. 2018; Jablonski 2020; Love et al. 2022). Thus, in the special circumstance when selection (i.e., an opportunity) is aligned with such (viable) lines of genetic least resistance in Schluter’s (1996) sense, integration rather than modularity might promote greater evolvability (see also Evans et al. 2021, and Voje et al., chapter 14, on instances where highly integrated traits appear to have been most evolvable). These contingent aspects of modularity would seem to disallow generalizations, and macroevolutionary predictions become difficult, although retrospective understanding of a role for modularity in specific cases is not a trivial insight.

Despite these issues, the ubiquity of mosaic evolution (the evolution of different characters at different rates), and more broadly, of incompatible character transformations across phylogenies (Jablonski 2017a), indirectly supports the view that evolution is more often facilitated by the ability of traits to change independently. Furthermore, among-clade differences may exist: arthropods seem to be masters of modularity, not just in terms of dissociating

morphological modules for independent growth and transformation (e.g., Nijhout and McKenna 2017), but perhaps also at the molecular level. For example, arthropods apparently more readily deploy the *Distal-less* pathway in new locations to generate novel structures (e.g., horns, wings: see Shubin et al. 2009; Bruce and Patel 2020) than do tetrapods, with the arthropod pathway largely dedicated to regulating outward growth but the vertebrate homolog *Dlx* involved not just in the early development of limbs, but in the placenta, forebrain, branchial arches, and other tissues (Panganiban and Rubenstein 2002; Sumiyama and Tanave 2020).

A related view sees evolvability as a positive function of the dimensionality of form (Vermeij's 1974 argument), which need not be directly related to modularity per se: Limpet shells can be described by fewer mathematical parameters than can helically coiled shells with complex apertures, and thus have lower dimensionality, but different snail lineages have not been analyzed from this perspective (for more on the positive associations between dimensionality and the rate or extent of diffusion in morphospace, see Foote 1991, 129; Pie and Weitz 2005, E9; Holzman et al. 2011 on evolvability as a positive function of the number of traits determining organismal performance). In a sense this is a “degrees of freedom” hypothesis: More components mean more avenues to evolve along, or, in Vermeij's (2015) view, for alleviating functional trade-offs.

Central to all these ideas from a macroevolutionary perspective is the still-open question of the long-term stability of genetic and phenotypic modularity (see Urduy et al. 2013), and how to operationally distinguish modules maintained by intrinsic factors resistant to change from those maintained by selection and thus readily altered at these large scales. Here too, retrospective macroevolutionary analyses of clades with demonstrable present-day differences in modularity would be a powerful merger of paleontological and neontological data. Ideally, we could compare two clades differing in modularity but presented with a similar opportunity, such as survival of a mass extinction, or arrival in a relatively unoccupied archipelago or larger landmass (potential examples, still lacking the paleontological dimension, include Galapagos finches versus mockingbirds, and Hawaiian honeycreepers versus thrushes; see Lovette et al. 2002).

Given the array of skeletal types that constitute almost all of the fossil record, we might ask whether developmental and evolutionary modularity—and thus potentially evolvability—differ across body plans involving many-element, articulating skeletons (e.g., vertebrates, echinoderms, and arthropods) and those having just one or two discrete elements and accretionary growth (e.g., corals, mollusks, and brachiopods; see, for example, Edie et al. 2022). The remarkable range of molluscan shell shapes (that is, scaphopods, nautiloid cephalopods, chitons, snails, and bivalves) and ornamentation patterns suggest exquisite local control in the sheet of tissue that generates those shells; but does the extra level of morphogenetic control and interaction afforded by articulating skeletons create a correspondingly enlarged evolvability at macroevolutionary scales?

An even more profound difference between clades that could be viewed from the modularity/evolvability standpoint involves lineages that sequester the germ line early, versus the plants and clonal colonial animals that sequester the germ line late and so can incorporate somatic mutations into gametes (Schoen and Schultz 2019 and references therein; C. Simpson et al. 2020; Yu et al. 2020). With late sequestration, each plant bud or animal zooid is potentially both a developmental and an evolutionary module, so that novel variants can originate within

the colony and propagate both sexually and asexually, conceivably increasing clade evolvability relative to early-sequestration clades. This notion might seem to contradict a widely (though not universally) accepted case of higher-level selection for evolvability: the pervasiveness of sexual reproduction across the tree of eukaryotic life. The Red Queen hypothesis for the maintenance of sex (e.g., parasite-mediated selection for the continual production of novel phenotypes) defines a process playing out at the population, species, and/or clade level (Van Valen 1975; Stanley 1979, 213–227; Nunney 1989; Sterelny and Griffiths 1999, 208–210; Hansen 2011) and thus is a decidedly macroevolutionary hypothesis. But there need not be a contradiction here: Species in most eukaryotic clades that reproduce asexually or parthenogenetically are also capable of sexual reproduction. Testing a macroevolutionary hypothesis of the consequences of evolvability as imposed by sex could involve asking whether lineages in which sexual reproduction is rare or involves a limited number of individuals are less prolific phenotypically than lineages in which sex is the norm. Because sexually produced individuals or colonies can be distinguished from asexually produced ones in several well-fossilized groups (foraminiferans, corals, and bryozoans), this question could be addressed empirically.

17.3.2 Ontogenetic Allometry or Multiphase Life Cycles

As already noted, developmental integration might promote long-term evolvability when the resulting trait covariation is aligned with internal and external selection, and a few analyses have provided examples (e.g., Navalón et al. 2020 on bird craniofacial evolution; Hedrick et al. 2020 on bat cranial evolution). Such covariation may reach its richest macroevolutionary potential in clades that undergo strong changes in form during ontogeny, as continuous variation in ontogenetic allometry (e.g., see the origin of sand dollars [Smith 2001] and brittle stars [Thuy et al. 2022]), or discontinuously in multiphase life cycles. As long recognized (e.g., Gould 1977), such clades have often evolved along ontogenetic trajectories via heterochrony (i.e., evolutionary changes in developmental timing), and in at least some cases, they traverse significantly greater volumes of morphospace than do clades with lesser allometries or more direct development. These clades include canids (e.g., Geiger et al. 2017; Machado et al. 2018, 1413; and for a broader overview, see Sánchez-Villagra et al. 2017), dinosaurs (Chapelle et al. 2020), angiosperms (Armbruster, chapter 15), and perhaps most famously, extant and fossil salamanders that retain larval traits, with modularity clearly a critical part of this capability (see Johnson and Voss 2013; Urdy et al. 2013; Fabre et al. 2020).

17.3.3 Novel Traits

Evolutionary novelty in the broad sense often seems to increase evolvability by creating new features for further variation and allowing clades to access new adaptive zones (G. Simpson 1944): the origin of limbs, lungs, the amniote egg, and feathers are certainly associated with an expansion in the morphological disparity (and taxonomic diversity, and functional repertoire) of the clades bearing them. However, we have surprisingly few robust examples of this key-innovation phenomenon, in which a novel feature directly triggers diversification (see Rabosky 2017, Martin and Richards 2019, and Erwin 2021a for catalogs and critiques of the many definitions of “key innovation”). Many putative key innovations have proven to be part of a chain of derived characters, or associated with “key opportunities” (i.e., extrinsic events), prior to phenotypic expansions (Donoghue and Sanderson

2015; Stroud and Losos 2016; Jablonski 2017a). Such contingencies are most clearly seen in macroevolutionary lags, the geologically long interval between the inception of a novelty or clade and its taxonomic or phenotypic diversification (Jablonski and Bottjer 1990), which appears to be widespread or even the general rule (Jablonski 2017a; Halliday et al. 2019; Kröger and Penny 2020; Ramírez-Barahona et al. 2020; Simões et al. 2020; Erwin 2021a). Such lags can provide a novel framework for evaluating intrinsic and extrinsic factors; they are generally tracked using taxonomic diversity, however, and more analyses are needed that treat them in morphospace and incorporate functional variety (as in Slater 2013 and Folk et al. 2019).

We do not know how often evolutionary novelties in the strict sense—that is, a trait lacking a homolog in the ancestor (G. Wagner 2014)—also fail to trigger diversification. As these true novelties often define clades, analyses of lags will need to operate across broad evolutionary trees, but effects seemingly imposed by intrinsic constraints and their removal or absence may also present a useful set of test cases. For example, mammals are highly constrained in the number of cervical vertebrae (Galis, chapter 16), but it is unclear, and worth testing, whether this constraint has impaired mammalian functional or morphological evolution relative to tetrapods that have circumvented it, such as sauropod dinosaurs, plesiosaurs, and long-necked birds (Müller et al. 2010; Taylor and Wedel 2013; Marek et al. 2021).

Another intriguing modification of development, little considered from the standpoint of evolvability, is the breaking of bilateral symmetry, which has occurred throughout plant and animal phylogeny, by a variety of developmental mechanisms (Palmer 2004). Bivalve mollusks are a system that would reward macroevolutionary analysis, as most species are bilaterally symmetrical, aside from small developmental adjustments allowing interlocking, hinged valves (Moulton et al. 2020; recall that the plane of symmetry lies between the two valves, not down the midline of a single valve). Some bivalve clades have strongly diverged from bilaterality, including the extinct, perhaps photosymbiotic, rudists, which evolved a conical-cylindrical right valve and a cap-shaped left valve, among other configurations (Jablonski 2020). Oysters, spiny oysters, scallops, and others have also shed bilateral symmetry in impressive ways (Nicol 1958), with extinct oysters showing a much wider range of shell geometries than do extant species, including planispiral, helical, and conical forms (Seilacher 1984). As many of these lineages are in the Order Pteriomorpha, the question arises whether this clade weakened bilateral patterning early in bivalve history and then could adopt asymmetry according to later opportunities or pressures, and thus had greater evolvability than related bivalve clades.

A shift from radial to bilateral symmetry is associated with a striking contrast in apparent evolvability in sea-urchin history (figure 17.1). The ancestral condition is radial, and the survivors of the end-Paleozoic mass extinction inherited that state, continuing to evolve as the group informally termed “regular” echinoids; they gave rise to many species but remained confined in morphospace. However, one lineage diverged to become the irregular echinoids, a bilaterally symmetrical, burrowing clade that eventually split into two branches typified respectively by heart urchins and sand dollars. The regular and irregular echinoids each contain ~500 extant species, but the irregulars have explored a much broader range of morphospace (Hopkins and Smith 2015). Understanding the developmental basis of this contrast, including a potential change in modularity (López-Sauceda et al. 2014; Saucède et al. 2015),

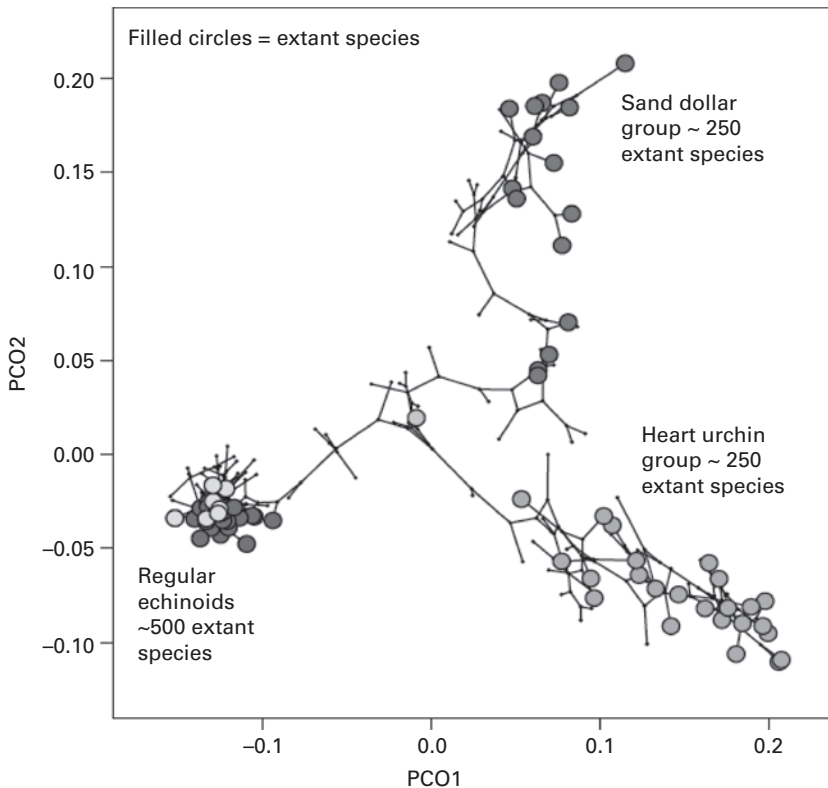


Figure 17.1

Differences in apparent evolvability in the major sea-urchin clades, portrayed in a phylomorphospace based on principal coordinates analysis of a character matrix. Modified after Hopkins and Smith (2015), used by permission.

and then testing an intrinsic evolvability hypothesis against alternatives—for example, ecological opportunities afforded by adoption of the burrowing, deposit-feeding habit—would create an exceptional model system for exploring macroevolutionary issues. One factor may be a profound developmental change near the origin of irregulars (Smith 2005) that allowed their plates to grow predominantly in place throughout ontogeny (as opposed to ontogeny via a combination of plate growth and insertion in regulars), making it easier to differentiate the upper and lower surfaces of the test, and thus to become burrowers, or, as in sand dollars, to use the upper surface as a feeding sieve. Shifts from radial to bilateral symmetry may also promote diversification in angiosperms, separately or in combination with other traits (O’Meara et al. 2016; Armbruster, chapter 15; but see Vamosi et al. 2018), but the effect has only been evaluated in terms of species richness and not phenotypic evolvability. Comparative analysis of floral evolution in morphospace according to floral symmetry would be a valuable next step.

Finally, the converse of a macroevolutionary lag is the dead-clade-walking phenomenon, where a clade suffers a sharp decline (e.g., during a mass extinction) and then persists for some time without rediversifying (Jablonski 2002). Like macroevolutionary lags, such clades appear to be widespread (Barnes et al. 2021), and just as lags appear to signal a

related gain in apparent evolvability, the dead-clade-walking pattern may signal a clade's loss of evolvability, or more precisely, these clades are potential natural experiments in the *loss* of traits thought to promote evolvability, for comparison to clades that retain those traits. As with lags, many of the “dead clades walking” may actually involve extrinsic factors, such as limits imposed by competitors or predators in the post-extinction world, but analyses are lacking. These clades have only been analyzed taxonomically, so that we still need to know whether they are phenotypically or functionally static after their bottleneck, and thus provide a vehicle for directly testing hypotheses on drivers of evolvability. However, if they shift significantly through morphospace despite low taxon numbers, they could not be viewed as suffering diminished evolvability in the sense used here.

17.3.4 Genome Size

For plants, genome size, and specifically, whole-genome duplication (WGD) related to interspecific hybridization and allopolyploidy, has been tied to evolvability. Allopolyploids can create unique amalgams of parental phenotypes and generate novel features (e.g., Soltis et al. 2014; Alix et al. 2017), so that plant clades more prone to allopolyploidy, and/or with more WGDs in their history, should traverse or occupy more morphospace than other clades do. This prediction is evidently met on a broad scale among the major angiosperm clades (Clark and Donoghue 2018). Much more work is needed to test the potential mechanistic link (e.g., see Zenil-Ferguson et al. 2019), and the macroevolutionary role of genome size in animals is even less clear. Ancient WGDs have been associated with early taxonomic and morphological diversifications in vertebrate and invertebrate clades (e.g., Conant 2020; Liu et al. 2021), but for vertebrates, at least, such duplication events are often followed by extended macroevolutionary lags (Glasauer and Neuhauss 2014; Davesne et al. 2021), and these events may even impede diversification (Kraaijeveld 2010), raising questions about a causal role.

What plants and animals do share is the potential to track genome size directly in the fossil record, allowing for more rigorous analysis without reliance on ancestral character-state estimation from extant species (animals: Thomson and Muraszko 1978; Organ et al. 2007, 2011; Hunt and Yasuhara 2010; Davesne et al. 2021; plants: Masterson 1994; Lomax et al. 2014; McElwain and Steinthorsdottir 2017). Of course, genomes can enlarge for reasons other than duplication, and one potential direction for macroevolutionary investigation in this area is the relative impact of transposon proliferation and WGD on clade survivorship and diversification, which might be assessed retrospectively when phylogenetic analysis shows a constant ploidy level, but fossil data indicate shifts in genome size. There are many ideas on the evolutionary role of mobile elements, some of them plausible, including the potential for cross-level conflicts, but the macroevolutionary impact of among-clade differences in transposon content—active or not—remains uncertain.

17.3.5 Elevated Speciation Rates

Over geologic timescales, most species tend to be morphologically static (i.e., oscillate within limits) or nondirectional over their histories, affording speciation a potential role in the extent and direction of morphospace occupation for many clades (e.g., Gould 1982; Hunt 2007; Jablonski 2017b; and from a very different perspective, Gorné and Diaz 2019). Some authors include high speciation rates in their definition of evolvability (e.g., Hedrick et al. 2020) although I argued against such a broad definition in section 17.2. In any case, we can ask

whether clades having higher speciation rates for intrinsic reasons—that is, owing to traits that increase the probability of reproductive isolation (see Jablonski 2008a for an inventory)—have higher rates or extents of net morphospace occupation. (Such analyses will not be circular if performed with care, even in the fossil record, where speciation is necessarily recognized phenotypically, because the critical variable is *net* differences in morphospace occupation.) A rough correlation between speciation rate and morphological change is seen for many clades at various points in their histories, albeit with considerable heterogeneity and an array of counterexamples (Stanley 1979; Rabosky et al. 2013; Crouch and Ricklefs 2019; Cooney and Thomas 2021, and many more citing and cited in these publications; see section 17.4.1 for temporal changes, such as early bursts).

The potential association between speciation and morphological change is relevant to evolvability for at least three reasons.

(1) Speciation may tend to occur preferentially in the direction of intraspecific variation (Hunt 2007; Love et al. 2022), providing a potential link between standing variation and both developmental bias and macroevolutionary evolvability, with high-speciation clades moving more rapidly across morphospace per unit time, and doing so more efficiently in that fewer species go in the opposing direction over the course of the trend—what Gould (1982) called a direction bias in clade dynamics (see also Jablonski 2020). The potential role of speciation rates in evolvability may depend on the shape and stability of the variational envelope around the taxa within a clade (e.g., Haber 2016; Watanabe 2018), including the resistance of that envelope to external pressures, but little is known about among-clade intrinsic differences that determine such features at this scale, or their mechanistic underpinnings.

(2) Traits can hitchhike on high speciation rates, proliferating in the clades that generate more species per unit time (see Jablonski 2017b). Thus, any attribute that tends to confer high speciation rates, such as low dispersal ability (see Jablonski 2008a; and for a recent discussion on birds, Tobias et al. 2020), might promote the proliferation of other traits that happen to covary with it among lineages. This hitchhiking aspect of species selection in the broad sense is likely to be widespread (Jablonski 2017b; Polly et al. 2017), so that the apparent evolvability of a trait, or of a clade, should be analyzed in a framework that takes both direct organismic selection and this indirect, cross-level effect into account.

(3) Directionality aside, clades having high speciation rates potentially generate more phenotypic experiments per unit time than low-rate clades. And if high-speciation clades tend to *accumulate* species, all else being equal, this will tend to reduce the clade's extinction risk and thus extend its duration, giving the clade more time to explore morphospace. However, counterexamples are well documented, particularly situations where high speciation rates lack commensurate expansions in morphospace (see the discussion of “non-adaptive radiations” in Rundell and Price 2009; Czekanski-Moir and Rundell 2019); even clades showing considerable movement through morphospace via speciation may ricochet within a confined portion of the space, as for the “regular” urchins in figure 17.1. Further undermining a simple relation between speciation rates and evolvability, high speciation rates are often accompanied by a “macroevolutionary trade-off” (Jablonski 2008a, 2017b), in which traits that confer high speciation rates also impose high extinction rates (e.g., Gould and Eldredge 1977; Stanley 1979, 1990; Van Valen 1985; Valentine 1990; Marshall 2017). Nonetheless, blanket statements that “diversity and disparity appear to be fundamentally decoupled” (Oyston et al. 2015; Guillerme et al. 2020; and many more) are an

oversimplification. The observation is certainly true for a single moment in geologic time, such as the present day, but the dynamics are more complex. The two currencies can accrue at different rates and even at different times, as implied by macroevolutionary lags, but when disparity increases, it tends to do so via branching events (i.e., via taxonomic diversification). Thus, while the wide range of potential relationships between diversity and disparity is crucial for understanding the evolutionary process, there is an important mechanistic association, albeit an imprecise one, and a more nuanced, quantitative approach is needed.

Given the broad range of potential relationships between speciation and a clade's movement or expansion in morphospace, the clades with the greatest evolvability might be viewed as the ones that disproportionately explore morphospace relative to their speciation rates. Broad morphospace occupation relative to species numbers at a point in time can also be produced by extinction (either random with respect to position in morphospace or against "average" morphologies; see Foote 1993, 1996), inflating the apparent relationship between diversity and disparity, so that time-series using fossil time-slices in diversity-disparity plots is the most informative approach (Jablonski 2017b; Wright 2017; see also P. Wagner 2010). This method has mostly been applied to clades originating under differing conditions (figure 17.2), but comparative analyses of clades responding to the same opportunity, advocated above, would be a valuable extension—for example, revisiting Eble's (2000) work comparing holasteroid and spatangoid echinoids, or the contrasting echinoderm clades in the Cambro-Ordovician interval (Deline et al. 2020). Testing potential factors in evolvability, clades having greater modularity or stronger ontogenetic allometry (for example) might tend to fall well above the diagonal in figure 17.2, while less modular or more isometric clades lie below or closer to it.

This diversity-disparity approach can also shed light on how evolvability changes over the history of a clade, by indicating where phenotypic productivity exceeds the stochastic

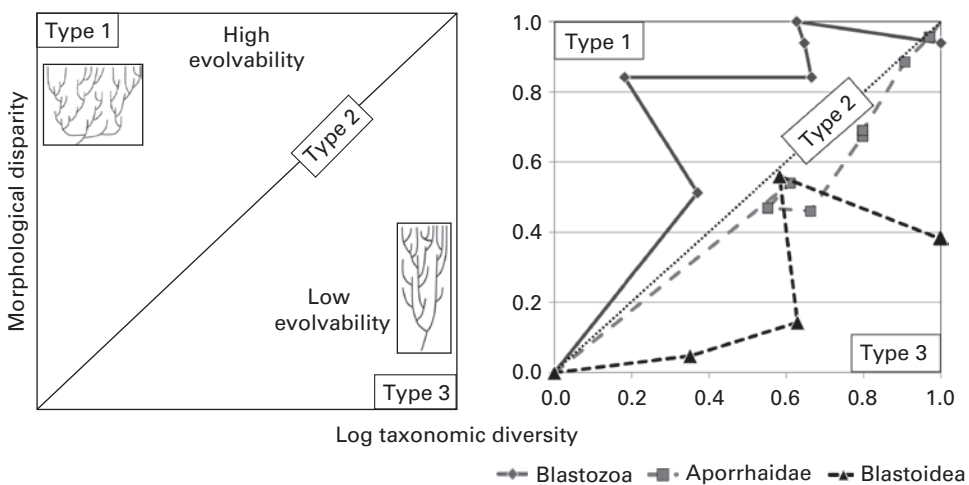


Figure 17.2

Evolution in diversity-disparity space. (Left): Type 1, morphology outstrips taxonomic diversification; Type 2, morphology is concordant with taxonomic diversification; Type 3, morphology trails behind taxonomic diversification. (Right): 3 empirical trajectories, for Cambrian-Ordovician blastozan echinoderms, Jurassic-Cretaceous aporrhaid gastropods, and Ordovician-Carboniferous blastoidean echinoderms. From Jablonski (2017b), which cites sources.

expectation from taxonomic diversification. For example, an early pulse of phenotypic invention might be followed by later confinement in morphospace (i.e., shifting from the upper left to lower right in figure 17.2, as implied in many studies, e.g., Cooney et al. (2017) on bird bill evolution). Alternatively, such a burst might be followed by diffusion in morphospace more proportionate to taxonomic diversification, trending from the upper left in figure 17.2 toward the diagonal. If ecological opportunity is an important factor interacting with intrinsic evolvability, then combining and partitioning clades within functional categories may yield new insights, as in the underappreciated finding that carnivorous mammals as a functional group show a significant burst in form relative to taxonomic richness after the end-Cretaceous extinction, but the constituent clades individually do not (Wesley-Hunt 2005).

17.4 Temporal and Spatial Patterns: Intrinsic or Extrinsic Factors?

Evolvability does not appear to be constant in time and space. The most frequently cited temporal patterns involve greater evolvability in early metazoan history, and at the inception of clades, regardless of their absolute geologic age. Such changes within time series may be best assessed as disparity relative to taxonomic diversity trajectories, as in figure 17.2, with high evolvability taken as a disproportionate occupation of morphospace relative to taxonomic richness in a time bin. Such discordance between diversity and disparity suggests that something unusual is going on, and as discussed below, the challenge is to separate intrinsic evolvability from extrinsic opportunities as the primary factor.

17.4.1 Temporal Patterns

Debates on the driver(s) of the Cambrian explosion of metazoan form, and its slowdown later in the Paleozoic and to the present day, are essentially asking whether evolvability has changed over time, on a grand scale. The evidence largely supports the view that major clades, and Metazoa overall, underwent a spectacular expansion of morphological and functional breadth in a geologically brief episode that significantly outpaced taxonomic diversification relative to later events in the history of life (Erwin and Valentine 2013; Jablonski 2017b; Deline et al. 2020, Erwin 2021b). However, mechanisms are still controversial: first, did intrinsic or extrinsic factors drive the rapid expansion in form and function, and second, what then slowed it down? Phylogenetic and paleontological data suggest that many of the developmental tools for building metazoans evolved well before the Cambrian, with a macroevolutionary lag that ended with an extrinsic trigger or opportunity, still not clearly identified (Erwin and Valentine 2013; Erwin 2021b). Thus the simple dichotomy between developmental (i.e., intrinsic) and ecological (i.e., extrinsic) mechanisms might be replaced by a “perfect storm” model of mutually reinforcing factors that successively fell into place, neither factor being sufficient on its own (Jablonski et al. 2017; Jablonski 2017b; see Love and Lugar 2013 for a tabulation of hypothesized mechanisms). Increases in gene-regulatory capacity certainly were associated with the Cambrian radiation (reviewed by Erwin 2021b), but much of that radiation appears to be associated with the redeployment and differentiation of existing developmental pathways. The failure to duplicate the Cambrian burst after the massive end-Permian extinction had been viewed

as an argument for a post-Cambrian decline in intrinsic evolvability (but see Foote 1999), very much in the spirit of the comparative approach suggested here. However, we now know that functional diversity barely dropped after the Permian event despite severe taxonomic losses (Foster and Twitchett 2014; Edie et al. 2018; and a truly pioneering study by Erwin et al. 1987), suggesting that post-Permian ecological opportunity was not comparable to that of the Cambrian. Most authors currently seem to view the slowdown of the Cambrian explosion in terms of ecological filling of marine habitats, but more extensive comparative studies of variation in Cambrian and post-Cambrian are needed.

At lower taxonomic levels, evolvability might decline over a clade's history, regardless of when it originated. This long-standing idea has mixed support: Harmon et al. (2010) detect few early bursts, Hughes et al. (2013) detect many, and Slater and Pennell (2014) attribute Harmon et al.'s result to a lack of statistical power. Integrating the early-disparity findings of Hughes et al. (2013) with the macroevolutionary-lag findings of Kröger and Penny (2020), superficially contradictory but actually dealing in different currencies, should clarify matters, but several non-exclusive mechanisms might be operating. The rate of production of *new* character states does seem to slow in many clades, even when character-state transitions do not (Oyston et al. 2015). However, nearly all clades produce some new character states throughout their history, rather than reiterating old states after maximum disparity is reached (Oyston et al. 2015); if the slowdown is attributable to intrinsic reductions in evolvability rather than ecological crowding, this implies a relatively weak effect. The apparent tendency for taxonomic diversification to slow with clade age (Heno Diaz et al. 2019) is at least as consistent with crowding effects as with regular, among-clade changes in intrinsic factors such as evolvability.

Perhaps the most provocative evidence for declines in intrinsic evolvability during a clade's history comes from P. Wagner's (2018) analysis of character-state correlations in the fossil record. Data from a large set of character matrices support a model breaking up correlations among characters and forming new ones, arguably analogous to reorganizing the structure of phenotypic variances and covariances—the P-matrix (see Love et al. 2022)—and thus presumably the G-matrix. Developmental data are needed to test this “correlated change-breakup-relinkage” model, and a key question is whether these changing linkages unfold across the appropriate timescales and have the limiting effects on overall phenotypic change that appear to typify the clade histories analyzed by Oyston et al. (2015).

Others suggest that evolvability tends to *increase* through a clade's history. Vermeij (2015) argues that younger branches within major animal and plant clades explore a greater portion of morphospace than older ones, explaining this pattern in terms of selection to alleviate energetic tradeoffs. This view implies a ratcheting effect not seen in the analyses by Oyston et al. or P. Wagner cited above, but those data are at a much finer scale than Vermeij's examples. Vermeij argues that “versatility” (which as noted above includes but is not restricted to modularity) has increased overall through time; Goswami et al. (2014) also argue for a net tendency of modularity to increase and integration to decline—implying that the relinkage in P. Wagner's “correlated change-breakup-relinkage” model is more localized within the phenotype than the ancestral state. These are plausible viewpoints that require testing in a common framework. One unexplored possibility is that the increase and later decline of evolvability occurs only at the origin of clades that are founded via an evolutionary novelty *sensu* G. Wagner (2014), that is a trait lacking homology in

the ancestor or that has radically and irreversibly changed from the ancestral state. Testing for declines (or increases!) in apparent evolvability of clades that originated in this way, vs those that more clearly arose in the context of ecological opportunity, may be one way to integrate these rather heterogeneous arguments (Jablonski 2020). Comparative analysis could also use evolutionary accelerations after mass extinctions to differentiate evolvabilities among contemporaneous clades, to test for differences in expansions in form or function among clades of different ages when encountering the same post-extinction opportunity to test for clade-age effects.

17.4.2 Spatial Patterns

Hypotheses for spatial variation in evolvability have long focused on the tropics, stunningly rich in taxonomic diversity and phenotypes, and the fossil record presents an additional, unexpected pattern, with disparity repeatedly emerging in marine invertebrate clades in onshore habitats. Comparing clade dynamics in morphospace across latitudes is challenging in terms of data required and the need to control for the strong latitudinal bias in both paleontological and neontological sampling. Great caution is warranted when maxima in origination rates or standing diversity or disparity are found to lie in the best-sampled regions, usually in the present-day temperate zone, as biases can be so strong that standard methods for factoring them out are ineffective (Valentine et al. 2013). A study that factored out sampling bias in two different ways found a significant tendency for marine invertebrate Orders, as a proxy for significant evolutionary novelty, to originate in the tropics over the past 250 Myr (Jablonski 1993; Martin et al. 2007), although data were lacking to test whether higher taxa originated more frequently in the tropics on a per-species basis.

A far less intuitive pattern occurs along marine depth gradients. Orders of marine invertebrates, again used as proxies for evolutionary novelty, preferentially originated in onshore habitats, that is at depths regularly subject to storms or normal wave disturbance (Jablonski and Bottjer 1990, Jablonski 2005). This pattern is independent of clade-specific bathymetric diversity gradients, turnover rates, or origination frequencies of constituent genera or within-clade traits, with low-level lineages originating offshore in certain clades and therefore sometimes expanding onshore as well as offshore (see also Jablonski et al. 1997; Tomašových et al. 2014; Bribiesca-Contreras 2017; Franeck and Liow 2019). The lone morphospace analysis to date is consistent with this finding: two Orders of irregular echinoids show greater divergences in disparity at their onshore origins than seen within the clades at any depth once established (Eble 2000; it would be interesting to plot the branch lengths in Figure 1 against their bathymetric context). Early vertebrate clades also first appear onshore (Sallan et al. 2018, who unfortunately exaggerate differences with the invertebrate patterns).

As with many other aspects of this overview, we have some provocative patterns, potentially indicating greater evolvability in tropical settings, and in onshore marine environments. New kinds of data and analyses are needed to bring these results more fully into the framework discussed here, and then to address the fundamental question: are they driven by intrinsic factors, as tentatively proposed by Jablonski (2005), or are they promoted by the extrinsic environmental gradients that define them (e.g., Vermeij 2012)? In other words, do organisms, species, or clades that inhabit warm, shallow settings have properties that enhance evolvability, presumably indirectly selected for by those environments, or do those environments directly promote greater phenotypic change?

17.5 Conclusion

Taken together, the data do suggest that intrinsic factors can influence the rate and scope of morphological and functional evolution at large scales. However, major challenges remain in converting these suggestions into a rigorously defined field. Perhaps the central difficulty for macroevolution lies in separating the intrinsic factors from the multitude of potential extrinsic biotic and abiotic drivers in determining vacancies, boundaries, or extents of expansion or transformation in a clade's morphospace or functional repertoire. When extrinsic factors can be excluded or accounted for, the issue becomes how apparent intrinsic evolvability differences map onto the potential causes of evolvability differences explored here and elsewhere in this volume, and the consequences of those different causes for the persistence or evolutionary lability of clades.

The most powerful analyses will be comparative, with the operational approach advocated here involving tests for among-clade (and perhaps across-time) differences in responses to a shared opportunity, in a macroevolutionary analog to a common-garden experiment. New methods for integrating fossil and present-day data are becoming available, and for macroevolutionary purposes this integration will be essential; one aim of this chapter has been to show that there is much raw material and a growing toolkit for moving the field forward. Every among-clade comparison of morphospace occupation or functional diversification is the potential basis for a study of evolvability, particularly when the occupation pattern is informed by phylogeny or explicitly structured over geologic time. We need a more active two-way exchange, predicting macroevolutionary patterns from short-term evolvability estimates, and predicting short-term evolvability and its developmental and genetic underpinnings from macroevolutionary dynamics. Such an exchange should come closer to testing underlying mechanisms and how they play out on the macroevolutionary stage. Evolvability could then become a powerful bridge between micro- and macroevolution. This would not involve simple extrapolation from lower to higher levels, but a way to understand and systematize the many nonlinearities and indirect effects inherent in a multilevel system, as we now understand organic evolution to be.

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