

SCALE AND HIERARCHY IN MACROEVOLUTION

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Abstract: Scale and hierarchy must be incorporated into any conceptual framework for the study of macroevolution, i.e. evolution above the species level. Expansion of temporal and spatial scales reveals evolutionary patterns and processes that are virtually inaccessible to, and unpredictable from, short-term, localized observations. These larger-scale phenomena range from evolutionary stasis at the species level and the mosaic assembly of complex morphologies in ancestral forms to the non-random distribution in time and space of the origin of major evolutionary novelties, as exemplified by the Cambrian explosion and post-extinction recoveries of metazoans, and the preferential origin of major marine groups in onshore environments and tropical waters. Virtually all of these phenomena probably involve both ecological and developmental factors, but the integration of these components with macroevolutionary theory has only just begun. Differential survival and reproduction of units can occur at several levels within a biological hierarchy that includes DNA sequences, organisms, species and clades. Evolution by natural selection can occur at any level where there is heritable variation that affects birth and death of units by virtue of interaction with the environment. This dynamic can occur when selfish DNA sequences replicate disproportionately within genomes, when organisms enjoy fitness advantages within populations (classical Darwinian selection), when differential speciation or extinction occurs within clades owing to organismic properties (effect macroevolution), and when differential speciation or extinction occurs within clades owing to emergent, species-level properties (in the strict sense species selection). Operationally, emergent species-level properties such as geographical range can be recognized by

testing whether their macroevolutionary effects are similar regardless of the different lower-level factors that produce them. Large-scale evolutionary trends can be driven by transformation of species, preferential production of species in a given direction, differential origination or extinction, or any combination of these; the potential for organismic traits to hitch-hike on other factors that promote speciation or damp extinction is high. Additional key attributes of macroevolutionary dynamics within biological hierarchies are that (1) hierarchical levels are linked by upward and downward causation, so that emergent properties at a focal level do not impart complete independence; (2) hierarchical effects are asymmetrical, so that dynamics at a given focal level need not propagate upwards, but will always cascade downwards; and (3) rates are generally, although not always, faster at lower hierarchical levels. Temporal and spatial patterns in the origin of major novelties and higher taxa are significantly discordant from those at the species and genus levels, suggesting complex hierarchical effects that remain poorly understood. Not only are many of the features promoting survivorship during background times ineffective during mass extinctions, but also they are replaced in at least some cases by higher-level, irreducible attributes such as clade-level geographical range. The incorporation of processes that operate across hierarchical levels and a range of temporal and spatial scales has expanded and enriched our understanding of evolution.

Key words: origination, extinction, recovery, evolutionary trends, novelty, species selection, emergent properties, geographic range.

PALAEONTOLOGY has changed greatly since the founding of the Palaeontological Association half a century ago. We are back at the 'high table' of evolutionary biology (Maynard Smith 1984; Gould 2002; Ruse and Sepkoski in press), and are enjoying rich interactions with ecology, biogeography, systematics, developmental biology and even conservation biology. All of these disciplines, and more, now regularly incorporate serious considerations of history, scale and hierarchy, derived in part from palaeontology and its attempts to grapple with the prob-

lems of macroevolution. Here I use the term 'macroevolution' in the descriptive sense, for evolutionary phenomena above the species level. I am not concerned with debating the health or adequacy of the neodarwinian synthesis, which has focused heavily but never exclusively on within-species processes, and in any case has itself always been evolving. Instead, I will briefly review how the expansion of temporal and spatial scales and the use of a hierarchical framework permits a richer understanding of evolutionary processes.

SCALE AND HIERARCHY

Scale and hierarchy are essential components of the conceptual framework for macroevolutionary analysis. Evaluating the role of *scale* involves the predictability of long-term, large-scale outcomes from short-term, local observations. This can be termed *empirical extrapolation* (Jablonski 2005a). Empirical extrapolation appears to break down, for example, in the mismatch between the demonstrated potential of most populations for rapid net change and the prevalence of net morphological stasis in many lineages over long time-scales. This mismatch across scales need not require novel forces to limit phenotypic change over most of the duration of a species, but it shows that short-term, localized observations on the evolutionary responsiveness of living populations are poor predictors of species-level behaviour over millions of years.

Empirical extrapolation has its advocates and critics, but *theoretical extrapolation* is more bitterly contested (Jablonski 2005a). In its purest form, theoretical extrapolation goes beyond predictability of outcome to continuity of process, holding that organism-level selection, along with the other canonical forces of microevolution such as drift, is the exclusive focal level of evolution. By contrast, some authors have argued (convincingly, in my view) that the logic of natural selection and other evolutionary forces need not reside exclusively at the organismic level: differential success of heritable variation owing to interaction with the environment, the Darwinian dynamic, also occurs at higher and lower levels. An evolutionary theory that incorporates processes operating simultaneously at multiple levels, with effects that can cascade upward and downward among levels, may be more difficult to grapple with than a single-level theory, but this approach also provides a richer understanding of large-scale patterns and processes in the history of life. This hierarchical view of evolution is hardly radical these days (see reviews in, e.g., Jablonski 2000; Grantham 2001; Gould 2002), but here I will emphasize operational approaches to what has sometimes been viewed as a rather hazy or irrelevant abstraction.

The distinction between hierarchy and scale might seem obscure, but in ecology and evolution, at least, it is generally clear. Scale involves more or less arbitrary quantities of a given measure. Humans have created nested sets of scalar units for convenience (seconds, minutes, hours; millimetres, centimetres, metres), but these too are arbitrary, and the units are *categories* ('classes' in the philosophical sense) whose properties are constant regardless of context: a centimetre or a gram has the same length or weight, respectively, regardless of what is being measured or weighed. In a biological context, an increase in scale might involve samples of 10, 100 or 1000 organisms, or

samples of taxa encountered in quadrats of 10, 100 or 1000 km². By contrast, a hierarchy incorporates entities ('individuals' in the philosophical sense) linked in important ways: by a one-to-many signalling architecture (as in the military command structure, or the regulatory cascade of a developmental pathway) or physically nested within one another as in demes, species and clades, or communities, provinces and biomes (for an entry into the many fine shadings of this coarsely drawn distinction, see Mayr 1982; Salthe 1985; Valentine and May 1996; Valentine 2004; for example, the last two of these references would consider signalling architectures to be trees rather than hierarchies in the strict sense). A sample of 1000 organisms will show very different evolutionary behaviour depending on whether it is a sample of, say, *Homo sapiens*, and thus a minuscule fraction of a huge and complexly structured gene pool, or if they are simply all the animals in an arbitrary square mile of Chicago, which may include humans, dogs, cats, squirrels, pigeons, raccoons, monk parakeets and the occasional coyote. By contrast, the isolate represented by Chicago's invasive parakeet population has distinct biological boundaries in time and space, and (in the absence of significant influx of birds from the species' Andean home range) its own evolutionary trajectory; and this isolate resides at one level within a biological hierarchy, containing organisms below and belonging to a species and then a clade above.

SCALE

At the organismal level, a greater variety of data are available on the present-day biota than for any other time plane. From enzyme kinetics to courtship behaviour, many aspects of the phenotype are accessible only in extant forms, even among clades having high fossilization potential, and the neontologist has access to habitats and to spatial and temporal resolution that is virtually impossible in much of the rock record. This situation imposes a conceptual trap by promoting the assumption that the conditions and phenomena observed today, or monitored in an area small enough for experimental manipulation or intensive replicate sampling, are sufficient to understand all of the dynamics relevant to the present-day distribution or long-term behaviour of species and clades. As discussed below, this is clearly not so in many instances.

Temporal scale

Systematists now appreciate that an enlarged temporal window can greatly inform phylogenetic hypotheses,

revealing character states and state combinations unknown in living taxa, and the literature is rich in examples where tree topologies change with the addition of palaeontological data (see reviews by Padian *et al.* 1994; Smith 1998; Forey and Fortey 2001; Crane *et al.* 2004; Grantham 2004; Smith and Turner 2005). Molecular phylogenetic methods provide an independent (though hardly infallible) basis for inferring evolutionary tree topologies but are largely uninformative about the phenotypes residing at key nodes (e.g. Erwin *et al.* 1997; Erwin and Davidson 2002; Valentine 2006). As an extreme case, consider a cladogram for a cow, a toad and a fruit fly. Molecular data (among others) can accurately recover the topology of this tree but tell us little about the morphology of the ancestors at each node, or about the evolutionary trajectories downstream of these common ancestors. Comparative developmental analysis can shed light on evolutionary transformations, but the rampant co-option of regulatory genes can make inferences about nodal forms extremely difficult, giving rise in our example to a very wide range of potential morphologies for the common ancestor of the fly and the toad (i.e. the basal bilaterian; for discussion, see Valentine *et al.* 1999; Erwin and Davidson 2002; Valentine 2004, 2006). At a slightly shallower node in the metazoan tree, the 'living fossil' members of the ancient molluscan class Monoplacophora, which are limpet-like forms that are apparently the outgroup to the rest of the living conchiferans (bivalves, gastropods, scaphopods, cephalopods), were often used to infer character states at the start of the great molluscan radiations but are now understood to be highly derived relative to the Cambrian ancestors (Lindberg and Ponder 1996; Giribet *et al.* 2006; see also Crisp and Cook 2005 for a general discussion of the misleading use of extant members of early branches to infer ancestral character states). The origin of the tetrapod limb (Clack 2005; Shubin *et al.* 2006), the teleost tail (Forey and Fortey 2001) and the avian wing (Norell and Xu 2005; Prum 2005) all become clearer as instances of sequential, mosaic evolution embedded within a larger radiation when data are included for the extinct stem lineages leading to the respective vertebrate classes.

The inference of ancestral character states is not just an issue for very deep nodes in the history of life. Many comparative analyses of adaptation in extant species require not only a robust cladogram but also a set of inferred ancestral states for continuous characters. Inferences on these character states are highly model-dependent and are generally saddled with wide confidence intervals (e.g. Cunningham *et al.* 1998; for progress in this area, see Martins 2000; Pagel *et al.* 2004), but such inferences can be made more realistic whenever palaeontological data are available. Indeed, palaeontological data can both provide the necessary empirical foundation for

some clades, and test the power and accuracy of inferential methods with independent estimates of ancestral traits (e.g. Polly 2001; Webster and Purvis 2002*a, b*; Finarelli and Flynn 2006).

Analyses of ecological and evolutionary time series have yielded results opposite to the simplest extrapolationist expectations. For example, the web of ecological interactions and feedbacks should keep population variability in check, but even in living systems population variability generally increases over time, regardless of taxa, body sizes, trophic level, latitude or type of population dynamics (see, e.g., Inchausti and Halley 2001, 2002, who analysed 544 natural populations in 123 species over time-scales exceeding 30 years). On the other hand, whereas present-day populations show great responsiveness to directional selection over the short run, palaeontological observations on many species show a tendency to net stasis and fairly stable boundaries to phenotypic change through time (reviews in Jackson and Cheetham 1999; Gould 2002; Eldredge *et al.* 2005).

The enlarged temporal window afforded by palaeontological data can permit direct observation not just of ancient phenotypes but also of evolutionary dynamics that must otherwise be inferred mainly through static spatial distributions or the topology of cladograms of extant taxa. Analyses restricted to a single time plane can be powerful, but can also be misleading or yield multiple alternatives because almost always they must deal with *net* diversification rates rather than the fundamental dynamic variables of raw speciation and extinction rates. For example, plausible arguments can be made for either a positive or a negative relation between geographical range and speciation probability (see references in Gaston and Chown 1999 and Jablonski and Roy 2003). Resolving this conflict is difficult using neontological data, in part because profuse net speciation among narrowly distributed taxa is difficult to distinguish from fragmentation of once-widespread species into many daughters. Palaeontological data, however, can test per-taxon speciation rates against maximum geographical ranges of species within lineages, circumventing this problem and showing a highly significant *inverse* relation between geographical range and speciation rate, at least in marine gastropods (Jablonski and Roy 2003; see Text-fig. 1). If general, this inverse relation has interesting implications for diversity dynamics ranging from adaptive radiations to restoration ecology.

Enlarging temporal scale to encompass the late Pleistocene (still a brief time relative to the average duration of species in most clades) captures extensive environmental disruptions and dislocations that have serious implications for the evolutionary interpretation of the present-day biota. The most obvious, of course, is the extinction of the terrestrial megafauna: the size-frequency

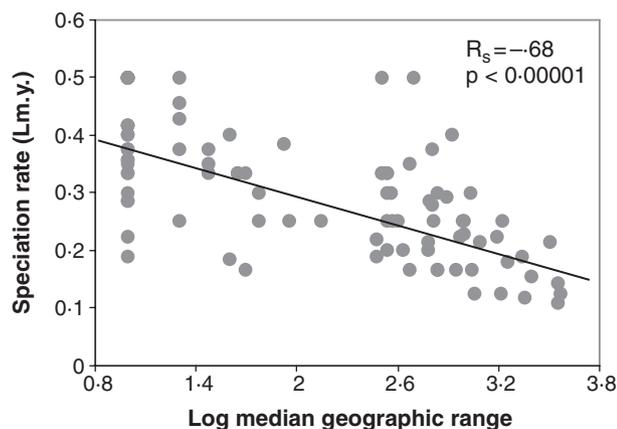
distributions of the tetrapod faunas on all continents, even Africa, have been significantly truncated since the Pleistocene heyday of mammoths, mastodons and ground sloths (see Barnosky *et al.* 2004; Lyons *et al.* 2004, and references therein). Evolutionary and ecological hypotheses that assume long-term stability in the size, abundance or taxonomic richness of terrestrial vertebrate communities must be framed with this geologically recent event in mind.

Expanding the temporal scale does far more than provide a glimpse of megafauna-rich Pleistocene communities. It gives abundant evidence for the spatial volatility of species distributions, with the individualistic behaviour of most species through the Pleistocene and Holocene generating transient associations that lack precise equivalents on the modern landscape (or more properly, giving rise to present-day associations that did not exist 12,000 years ago) (e.g. Bennett 1997, 2004; Jackson and Overpeck 2000; Davis and Shaw 2001; Lyons 2003, 2005; Jackson 2004; Jackson and Williams 2004; Willis and Niklas 2004; NRC 2005). Observations that species fail to exhibit total ecological anarchy (e.g. a failure to reject a null hypothesis of complete statistical independence) have been held to validate claims for 'community unity' over these timescales (e.g. McGill *et al.* 2005; Jackson and Erwin 2006; but note that McGill *et al.* 2005 found the shuffling of species associations to be *greater* than expected by chance!). This view seems to conflate phenomenology with underlying mechanism: independent movement of species having overlapping distributions is detectable only at the edges of their respective geographical ranges, which are rarely sampled palaeontologically, particularly in terrestrial systems (Roy 2001). Furthermore, species with similar climatic requirements will inevitably move in broadly similar directions during glacial-interglacial cycles even without strong biotic interactions; a null model that

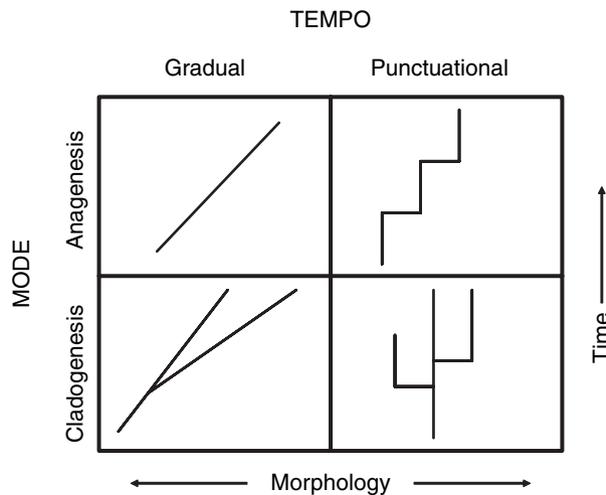
allows polar bears in Florida or hippos in Norway is too unrealistic to be meaningful (Jackson and Overpeck 2000; Jackson 2004; Lyons 2005). The apparent temporal coherence in these assemblages could just as readily be a passive consequence of sampling artefacts, overlapping tolerances and rates of displacement, although it should be noted that such coherence can still provide a context for longer-term interactions among limited sets of species. Only a few of the myriad ecological and evolutionary implications of these spatial dynamics have been explored in any detail (but see Roy *et al.* 1996b; Bennett 1997; Dynesius and Jansson 2000; Jansson and Dynesius 2002; papers in Willis *et al.* 2004; Thompson 2005); it is remarkable, for example, that so little has been done comparing the evolutionary responses of annual plants or short-lived rodents to those of clonal reef corals that may have been through only a dozen generations (as measured by genetic individuals) since the last ice age (Potts 1984). The implications of community disassembly are increasingly germane to present-day ecosystems as climate changes begin to create mismatches between predators and prey, pests and controls, hatchlings and critical resources (e.g. Stireman *et al.* 2005; Bradshaw and Holzapfel 2006).

Expanding temporal scales to the 10^6 – 10^7 year time-frame encompasses a wealth of phenomena outside the range of empirical extrapolation. The most famous of these is the extraordinary frequency of net evolutionary stasis through the history of morphospecies despite the short-term malleability of most populations. Many mechanisms for stasis have been proposed, and they are probably less mutually exclusive than generally assumed (for additional recent reviews, see Hansen and Houle 2004 and Eldredge *et al.* 2005). An enormous literature exists on this topic, and I will make only two points here. First, all possible combinations of evolutionary tempo and mode (Text-fig. 2) have been documented in the fossil record: the fascinating challenge is to frame and test hypotheses for the distribution of those combinations among clades and environments (Jablonski 2000 and references therein). Second, analysis of species-level phenotypic change in the fossil record is not a trivial task when confronted with the realities of sampling and environmental change in real sections, and the limits imposed a kind of Palaeontological Uncertainty Principle (Jablonski 2000), the frequent tradeoff between temporal resolution and spatial coverage. Happily, recent developments in methods for analysing species-level phenotypic change dynamics in the fossil record bode well for future research in this area (e.g. Bush *et al.* 2002; Kidwell and Holland 2002; Roopnarine 2003, 2005; Hunt 2004; Hannisdal 2006).

Another striking failure of empirical extrapolation comes when the expanded temporal scales include alternative global states, such as greenhouse worlds, or



TEXT-FIG. 1. When the observational scale is expanded to the myr timescale, speciation rate per species per myr (Lm.y) is inversely related to median geographical range of constituent species (from Jablonski and Roy 2003).



TEXT-FIG. 2. All possible combinations of evolutionary tempo and mode have been recorded from the fossil record. Research is sorely needed on whether clades vary in their frequencies of the different combinations, and if so, why. The upper left quadrant is classic phyletic gradualism, and the lower right is punctuated equilibrium.

extreme events, such as those that drive certain mass extinctions. Because mass extinctions and their aftermath involve both scalar and hierarchical effects, I will defer their discussion until the end.

Spatial scale

Palaeontology has tended to focus on two highly disparate spatial scales: local stratigraphic sections or suites of nearby sections on the one hand, and the global synoptic record on the other. However, analyses at intermediate, regional scales have much to offer. Spatially heterogeneous dynamics have now been recorded for many macroevolutionary events, including the Ordovician radiations, the marine Mesozoic revolution, recoveries from the end-Ordovician, end-Permian and end-Cretaceous mass extinctions, and the demise of the Pleistocene megafauna (Roy 1994, 1996; Miller 1997a, b, 1998; Jablonski 1998, 2005a; Martin and Steadman 1999; Barnosky *et al.* 2004; Krug and Patzkowsky 2004; Lyons *et al.* 2004; Twitchett *et al.* 2004; Aberhan *et al.* 2006). In each of these instances, the availability of spatially explicit data gives rise to new hypotheses: that the Ordovician radiations may have been promoted by tectonic activity, that the Mesozoic revolution may have been mediated by regional changes in climate and nutrient inputs, and that recoveries from mass extinctions involve not only *in situ* evolution but also biotic interchanges, with invasion intensity varying among regions.

Even the latitudinal diversity gradient, the most pervasive biological pattern in the global biota, appears to be

shaped significantly by interregional dispersal, contrary to the widespread assumption that *in situ* diversification predominates (e.g. Jablonski 1993; Wiens and Donoghue 2004; Jablonski *et al.* 2006). More generally, spatially explicit palaeontological data show that present-day distributions can be a poor indicator of the past deployment of clades. Seemingly clear-cut congruencies between phylogeny and large-scale biogeography, from the now-exclusively New World anteaters and hummingbirds to the now-exclusively Southern Hemisphere ratites to the now-exclusively Old World bananas and rhinoceroses, have been falsified by fossil evidence for past distributions outside present-day geographical ranges. Even the famed Gondwanan distributions of plants and animals across the southern continents now appear to have arisen in part by relatively recent trans-oceanic dispersal rather than fragmentation of the supercontinent (for recent reviews, see de Queiroz 2005; Waters and Craw 2006). Such evidence may be inconvenient for vicariance biogeographers, but such dispersal events, and presumably regional extinctions, are probabilistic and not truly random (contrary to the most ardent advocates of vicariance biogeography; see Cook and Crisp 2005 for discussion), and thus invite macroevolutionary study. The irony here is that the vicariance approach was developed to incorporate a dynamic earth in biogeographical analysis, but the biota is proving in many cases to be more dynamic than the earth beneath it. The macroevolutionary consequences of this biotic dynamism have still not received the attention they deserve.

Spatially explicit palaeontological data will also allow us to address the evolutionary implications for the scaling effects now recognized for many of the classic ecological patterns, such as diversity-productivity (Chase and Leibold 2002; Whittaker *et al.* 2003) and species-area relationships (and see Beever *et al.* 2006 for a more general review). The steepening of the species-area relationship (SPAR) with spatial scale probably represents a shift from situations dominated by immigration/emigration dynamics to those dominated by true origination and extinction (for an array of rather different versions of this argument, see Preston 1960, 1962; Rosenzweig 1995, 2004, 2005; Hubbell 2001; Allen and White 2003; Turner and Tjørve 2005; Drakare *et al.* 2006). Such scaling effects clearly have implications for understanding the relation between local diversity patterns and global dynamics, and the general failure of regional diversity dynamics to track estimated changes in habitat area (sampling artefacts aside) raises a host of interesting questions (e.g. Valentine and Jablonski 1991; McRoberts and Aberhan 1997; Crampton *et al.* 2006; see also Barnosky *et al.* 2005). The increase of the SPAR slope towards unity at continental scales, and the troublingly weak correlations over long time-scales, is interesting not only from a macroevolutionary perspective

but also for present-day conservation efforts. For example, the buffering effects implied by SPAR slopes much lower than 1 no longer apply when perturbations approach the province- and continent-wide scales confronting palaeontologists and conservation biologists (Rosenzweig 2005).

HIERARCHY

Lewontin's (1970) classic prescription for evolution by natural selection requires heritable variation in traits that influence fitness of units at a given level. Evolution thus involves both *replication* (reproduction of 'individuals' with heritability) and *interaction* (fitness differentials among 'individuals'), and many authors have argued that the interplay of those two processes can shape lineages at any hierarchical level (see discussions in Wright 1959; Lewontin 1970; Hull 1980, 1988; Gould 1982, 1985, 2002; Eldredge 1985, 1989; Salthe 1985; Brandon 1990; Grantham 1995, 2001, 2002; Valentine and May 1996; Sterelny and Griffiths 1999; Jablonski 2000, 2005a). The replicator-interactor model encompasses more than the canonical gene-organism couplet. For Hull (1980, p. 318), a replicator 'passes on its structure largely intact in successive replications', while an interactor 'interacts as a cohesive whole with its environment in such a way that interaction causes replication to be differential' (see also Hull 2001). The cohesion or discreteness of the interactor need not be absolute; indeed, such a requirement would exclude even organisms, the paradigmatic interactors: interactors thus reside at many levels in the biological hierarchy (e.g. Hull 1980, 2001; Eldredge 1985; Brandon 1990; Gould 2002). Nor does replication need to be precise: this would exclude genes subject to mutation and crossing over, so long as it yields descendants 'similar enough to respond similarly to similar selection pressures' (Hull 1980, p. 321). Thus, the mechanism of replication is less important than the descriptive, essentially statistical issue of heritability (Mayr 1982; Wagner 1988, 1990), which can also be addressed at any hierarchical level. Returning to Lewontin's formulation, selection can drive evolution at any level where (1) there is variation, (2) that variation influences reproduction and survival (= interaction at that level) and (3) the variation is heritable (= replication at that level). Such processes can run the gamut from DNA sequences that spread extra copies of themselves around the genome to, as discussed below, species whose extinction probabilities are determined in part by the species-level property of geographical range.

For the purposes of this discussion, consider three evolutionary processes that can occur simultaneously. First, there is differential survival and reproduction of bodies within populations by virtue of the interaction of those

phenotypes with the biotic and physical environment. This is conventional *Darwinian selection*, of course. Second, there is differential extinction or speciation (i.e. differential survival and reproduction of species within clades) by virtue of the interaction of the phenotypes of *bodies* with the biotic and physical environment. This is *effect macroevolution* as defined by Vrba (1980; Vrba and Gould 1986). Third, there is differential speciation or extinction (i.e. differential survival and reproduction of species within clades) by virtue of the interaction of the emergent properties of *species* (such as geographical range or genetic population structure) with the biotic and physical environment. This is *species selection* in the strict sense. The second and third processes are often grouped into broad-sense species selection, with the key criteria being emergent fitness at the species level, i.e. differential birth and death (replication) rather than emergent properties (interaction) at the species level (e.g. Stanley 1979; Gould 2002; see Grantham 1995 and Lieberman and Vrba 2005 for the complex history of these terms). Differential survival and reproduction may also operate at lower levels (e.g. the selfish DNA sequences and other intracellular passengers that operate as replicating parasites within the genome), at intermediate levels (e.g. when colonies of eusocial insects operate as emergent units of selection) and perhaps at higher levels (when the emergent properties of clades affect clade survival, although heritability and thus the efficacy of evolutionary trends via clade selection has not been much explored). The challenge is to identify emergent properties in a consistent way, and to test their roles empirically at different hierarchical levels.

Emergence

One relatively straightforward operational approach to identifying emergent properties is to treat a feature as emergent at a given level if its evolutionary consequences do not depend on how the feature is generated at lower levels (Jablonski 2000; Jablonski and Hunt 2006). This approach, which is similar to Brandon's (1990) application of the statistical concept of 'screening-off', has often been tacitly applied at the organismic level. For example, selection on wing size in laboratory *Drosophila* can produce equivalent changes either by changes in cell size or by changes in cell number (Robertson 1959 and many studies since). Because the organism was the focal level of the experiment, we know that the large-winged phenotype was the actual, and emergent, property under selection, and not the cellular or genetic underpinnings of this trait. The variation at lower levels was, in Brandon's terminology, screened off from selection at the organismic level.

Many properties have been ascribed to species, but not all of them are considered to be emergent. For example,

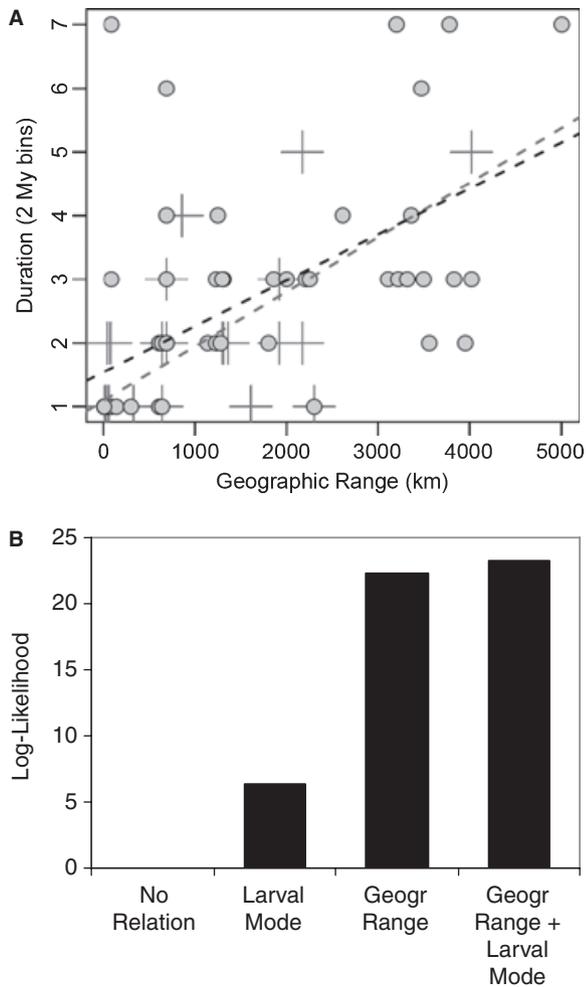
mean body size or pelt coloration may validly characterize species but are essentially statistical statements about organisms within the species; these have been termed aggregate properties to distinguish them from emergent ones (e.g. Vrba and Eldredge 1984). As already noted, effect macroevolution, in which organismic or aggregate features determine speciation or extinction rates, can still yield outcomes at odds with processes operating exclusively at the organismic level, as when organismic selection favouring large body size conflicts with higher species-extinction probabilities or damped speciation probabilities in large-bodied taxa (see Van Valen 1975; Jablonski 1996). The ecological literature on 'evolutionary suicide', sometimes less vividly termed Darwinian extinction, represents an independent realization that organismic selection can create conflicts across levels, in this case by driving organismic evolution in directions that increase extinction probabilities at the species and clade levels (see Webb 2003; Parvinen 2005; Rankin and López-Sepulcre 2005).

In contrast to body size, geographical range is widely regarded as an emergent property at the species level, inversely related to both extinction and speciation rates (see Jablonski 1987, 2000; Brown 1995; Grantham 1995, 2001, 2002; Sterelny and Griffiths 1999, p. 206; Gould 2002; Okasha 2003; Gregory 2004; Rice 2004, p. 312). Some have argued that benthic species' geographical ranges are really organismic traits because ranges are often significantly related to modes of larval development (e.g. Vermeij 1996; Levinton 2001, p. 402; Webb and Gaston 2005). This seems a bit like treating eyes as a genetic trait because their generation is significantly related to the expression of the *Pax6* gene, but this view also fails empirically on two counts. First, the relation between geographical range and molluscan species duration is significant even within developmental categories (Jablonski and Hunt 2006 and references therein) (Text-fig. 3A). Second, and more importantly, the evolutionary consequences of broad or narrow geographical ranges tend to be similar regardless of how those ranges are achieved at the organismal level, at least within broad groups such as benthic marine invertebrates. For example, widespread species of marine bivalves, gastropods, echinoids and bryozoans are geologically longer-lived than spatially restricted species, regardless of whether that broad range is achieved primarily via free-swimming larvae (as in gastropods and echinoids for the most part), rafted adults (as in bryozoans for the most part) or ecological tolerances of adults (evidently as in bivalves for the most part) (see Jablonski 1987, 2000; Cheetham and Jackson 1996; Jeffery and Emler 2003; Jablonski and Hunt 2006). It appears, then, that geographical range size is determined by a complex interaction of factors whose strengths vary among clades (e.g. Brown *et al.* 1996; Case *et al.* 2005;

Parmesan *et al.* 2005), and that these diverse factors underlying the variation in range size among species are screened off from (i.e. do not strongly influence) the macroevolutionary outcome (see Grantham 2007 for a deeper and more complete review of emergence in general and geographical range in particular). We can formally evaluate this argument using generalized linear models (GLMs), where larval mode and geographical range are tested as predictors of species duration against a model that incorporates both factors, thereby assessing the degree to which the effects of the putatively species-level trait (i.e. geographical range) on species duration are redundant with, and thus reducible to, the organismic trait (i.e. larval mode), and vice versa. For the Late Cretaceous data, adding geographical range to models containing only larval mode significantly improves model fit, whereas adding larval mode to models containing geographical range does not (Jablonski and Hunt 2006; Text-fig. 3B). These results not only support the view that geographical range is an emergent property irreducible to a single organismic trait, but also provide a general approach to evaluating hypotheses for the relative contribution of different properties to macroevolutionary dynamics.

Not only do geographical ranges (1) vary in size among species and (2) contribute significantly to (i.e. are significant correlatives of) species survivorship and origination rates, they are also (3) heritable among species in the sense that daughter species or clades resemble their ancestors more closely than expected by chance, as reported for marine molluscs, terrestrial birds and mammals, and herbaceous plants (Jablonski 1987; Ricklefs and Latham 1992; Brown 1995; Blackburn *et al.* 2004; Qian and Ricklefs 2004; Hunt *et al.* 2005, who provided a more robust analytical method than Webb and Gaston 2003 that effectively reverses their results; Purvis *et al.* 2005; Jablonski and Hunt 2006). This completes Lewontin's triad of prerequisites for evolution by selection at this higher focal level, as discussed at the start of this section. Furthermore, geographical ranges are heritable among species *within* developmental types for Late Cretaceous molluscs (Jablonski and Hunt 2006), allaying concerns that the pattern results solely from the heritability of larval modes (Webb and Gaston 2005, Text-fig. 4). (Species-level heritabilities could readily vary among clades, just as they do for organismic properties, and a rigorous treatment of this issue would be valuable; Hunt *et al.* 2005.)

The extent of strict-sense species selection is unknown: how many features of species, or for that matter of clades, are emergent by the operational criterion discussed here? and of those, how many are heritable? Every species has a geographical range, which immediately opens a large domain for the impact of emergent properties on clade dynamics: the burgeoning macroecological literature on



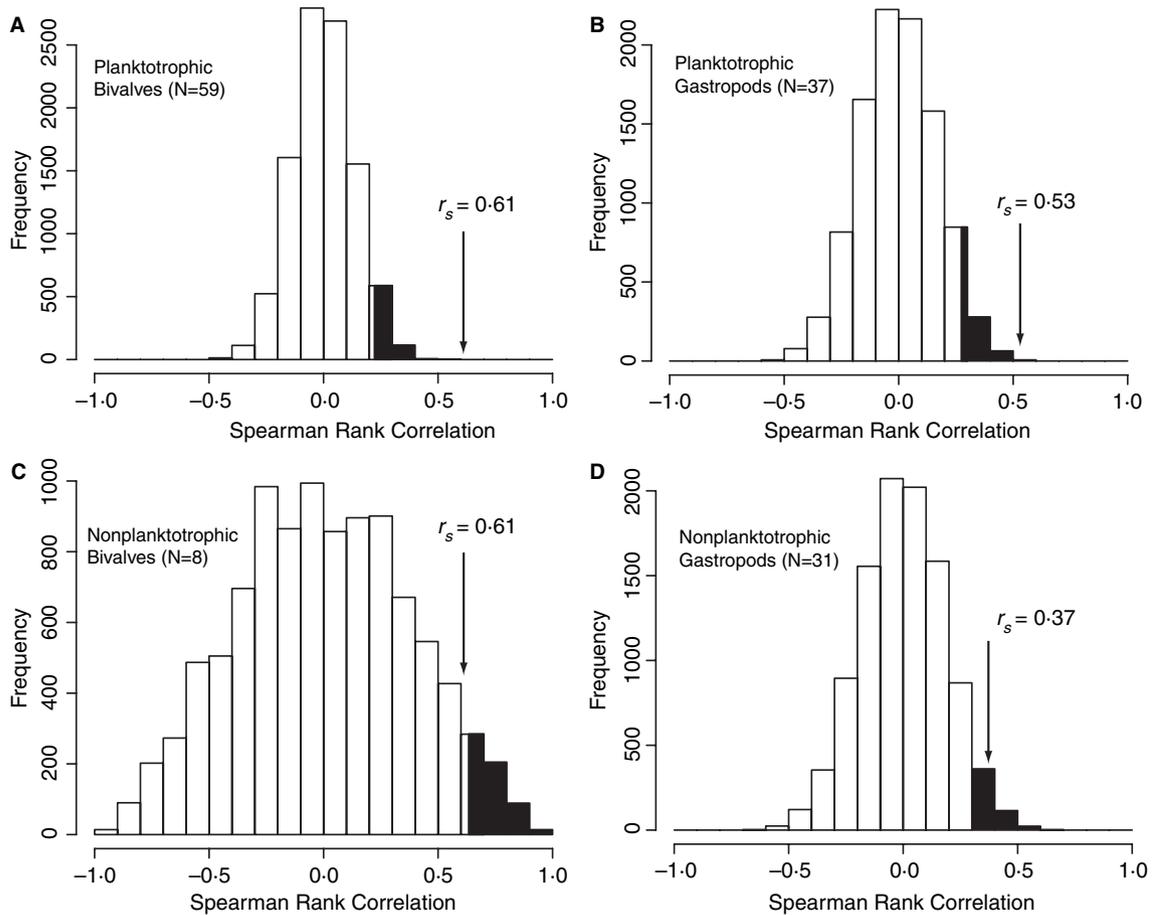
TEXT-FIG. 3. A, geographical range and geological duration are positively related for gastropod species within both planktotrophic (circles, slightly shallower regression line, $n = 55$) and non-planktotrophic (crosses, slightly steeper regression line, $n = 51$) modes of development. The two slopes do not differ significantly and are shown for comparative purposes; Spearman rank correlation 0.72 and 0.73, respectively (both $P < 0.0001$; see Hunt *et al.* 2005 for discussion of the resampling method used to assess significance). B, log-likelihood results from modelling stratigraphic duration as a function of geographical range and/or larval mode using generalized linear models. The log-likelihood of the simplest model, with neither factor contributing to duration, is set at 0, so that the values plotted indicate how much better each model is than the null. Larval mode does improve the fit relative to the simplest model, but the model using geographical range as the predictor performs much better, and there is only a slight, non-significant increase in log-likelihood when adding larval mode as a second predictor (see Jablonski and Hunt 2006 for details).

the causes and consequence of geographical range size (e.g. Gaston 2003) is a rich source of potential case studies. Several authors have generated tentative lists of additional species-level traits, from several aspects of

geographical range *shape* to genetic population structure to sex ratio (e.g. Vrba and Eldredge 1984; Jablonski 1986a, 2000; Vrba and Gould 1986; Vrba 1989, table 2; Maynard Smith 1998; Gould 2002; Stearns 2002; see interspecies differences in 'evolvability' as emergent traits according to Dawkins 1989!). However, these factors remain virtually untested.

On the other hand, species selection in the broad sense has been validated as a significant evolutionary process many times by both palaeobiological analyses and the widespread application of comparative methods to extant clades (as pointed out by Jablonski 2000; Coyne and Orr 2004). As noted above, most neontological sister-clade comparisons measure net diversification rather than raw origination and extinction rates, but they provide solid evidence for causal links between the differential waxing and waning of clades and the intrinsic biotic properties of their constituent organisms, populations or species (involving a huge range of traits from nectar spurs in angiosperms to geographical range sizes in birds) (see reviews in Freckleton *et al.* 2002, 2003; Coyne and Orr 2004; Paradis 2005). This is a literature begging to be systematically mined and extended for its larger macroevolutionary import.

The recognition of higher-level selection processes does not in itself complete a macroevolutionary theory. Selection at the organismic level is certainly a powerful force for moulding organismic adaptation, and broad-sense species selection appears to modulate the frequency and persistence of many adaptations. But the hierarchical structure of life imposes a more complex dynamic, because evolutionary processes can operate simultaneously at each level and can propagate upwards and downwards (in what is formally termed upward and downward causation from a focal level; see Campbell 1974; Vrba and Gould 1986). Thus, differential proliferation of a trait or a lineage at a given hierarchical level cannot simply be assumed to be driven by selection at that level. For example, upward causation might occur when the intragenomic proliferation of selfish genetic elements so disrupts the life cycle of their insect hosts that they increase extinction risk for infected populations so that the organismic traits of the host species suffer higher extinction rates relative to those of uninfected species (see Vinogradov 2003, 2004; Gregory 2005). In downward causation, profuse speciation of a snail subclade owing to subdivided population structure could increase the number of species with long spines on their shells relative to those with smooth shells; this process could reinforce organismic selection or it could drive proliferation of the trait even if it is approximately neutral in selective value at the organismic level. Such hitch-hiking effects may be important to the distribution of phenotypes within and among clades (a process termed species hitch-hiking by Levinton *et al.*



TEXT-FIG. 4. Species-level heritability of geographical ranges assessed using randomization of rank correlations for ancestor-descendant or sister-species pairs of A, planktotrophic and C, non-planktotrophic bivalves, and B, planktotrophic and D, non-planktotrophic gastropods from Late Cretaceous deposits of the Gulf and Atlantic Coastal Plain. Each histogram shows the distribution of Spearman rank correlations (R_s) generated by shuffling the geographical ranges of ancestors 10,000 times. This shuffling removes any heritability by separating ancestor-descendant pairs but preserves other aspects of the empirical distribution of range sizes. In each plot, the arrow shows the observed value of R_s relative to the 10,000 randomized values, with the 5 per cent one-tailed rejection region shaded black. (From Jablonski and Hunt 2006)

1986; Levinton 2001; see also Jablonski 2000, 2005a; Gould 2002). Much of the comparative biology literature is an attempt to grapple with this possibility, phrased in terms of phylogenetic effects, but it has rarely been tested palaeontologically (but see Wagner 1996).

The complexity of multilevel selection is tempered by the rules that typify dynamics within hierarchies. For example, the propagation of effects is asymmetrical: dynamics at lower levels need not impinge on higher levels but dynamics at higher levels must always propagate downwards (e.g. Salthe 1985; Valentine and May 1996). For example, a parasitic DNA sequence might never proliferate to the point of reducing the fitness of the host organism, and a fearsome disease might devastate Caribbean urchin subpopulations without fully eliminating *Diadema antillarum* or even significantly reducing the species' total genetic diversity (Lessios *et al.* 2001). For

that matter, 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 if the extinction probability of the species of an echinoid clade is increased, say by decreasing their average geographical ranges, the many organismic traits are at risk by downward causation, as are all the parasitic DNA sequences in their genomes.

Several other shifts in dynamics occur when moving up hierarchical levels. For example, the number of replicating units decreases going up the hierarchy so that chance effects may become more important. Such 'phylogenetic drift' or 'species drift' (Stanley 1979; Levinton *et al.* 1986; Levinton 2001; Gould 2002) has mainly been treated as a null model (e.g. Raup and Gould 1974; Raup 1981; Suter 1988; Wollenberg *et al.* 1996; Eble 1999), but clades containing just a few species at any one time are surely

subject to this process (which also requires heritability to have cumulative effects, of course). Characteristic rates of change also tend to decrease with each ascending hierarchical level (e.g. Allen and Starr 1982; Valentine and May 1996). Thus, the biased replication of selfish genetic elements with each cell cycle is rapid relative to the generation times of most metazoan organisms, which in turn are brief relative to the speciation rates of most metazoan clades ['instant speciation' via polyploidy being an exception that accounts for a surprising fraction of animal diversity (Gregory and Mable 2005) and more than 70 per cent of flowering plant species (Masterson 1994; Tate *et al.* 2005)]. This decrease in number and rate going up the hierarchy has been used as an argument against the evolutionary effectiveness of even broad-sense species selection (e.g. Fisher 1958), but such arguments hold only if the shaping of organismal adaptation is the sole evolutionary process or outcome of interest, and if one ignores the operation of upward and downward causation. Thus, although differential speciation or extinction may generally be too slow to construct a complex adaptation such as a wing (but see Rice 1995, 2004), dynamics at the species level can determine the persistence and number of genealogical units bearing wings within and among clades, and even the long-term persistence of such a trait.

Trends

Long-term directional changes appear to pervade the history of life at virtually all scales, from the stepwise transition from chemical to biological evolution through the increases in suture complexity of Palaeozoic ammonoids, in body size of Cenozoic horses and other mammals, in armour of post-Palaeozoic molluscan shells, and in hominid cranial capacity (e.g. McNamara 1990; McShea 1998a; Bambach and Knoll 2000; Gould 2002). The past decade has seen much progress on methods for evaluating trends in a hierarchical context. We now understand that such long-term changes can arise via a wide range of mechanisms, and that different dynamics can operate simultaneously, in opposition or in concert, at different levels. In simplest terms a trend may be underlain by transformation of its constituent species, by preferential origination of new species, by random speciation followed by differential survival or proliferation in the direction of the trend, or by any combination of these very different processes.

One major advance in our understanding of trends came with the recognition that many patterns could arise via passive diffusion from a fixed boundary, as when a clade originates near a minimum viable body size (e.g. Stanley 1973; Gould 1988, 2002; McShea 1994, 1998b, 2000). Such passive trends arise owing to the topography

of the adaptive landscape, and it will be useful to distinguish external selection and internal constraint in setting boundary conditions (e.g. McShea 2005). Alroy's (2000) expanded array of possible trend dynamics, with clades diffusing across a landscape complicated by additional attractors or adaptive peaks, can be viewed as variations on passive mechanisms (C. Simpson, pers. comm. 2006), although these complications undermine the standard tests for recognizing passive trends (see also Wang 2001, 2005). A further complication arises when trends are driven by protracted environmental changes, i.e. by evolution in a shifting landscape, as has been suggested for some long-term evolutionary size increases (e.g. Hunt and Roy 2006 and references therein). Far from corroborating Cope's Rule, which posits a pervasive, intrinsic advantage for large size (at least over the short term), these climate-driven patterns show just how context-dependent even large-scale trends can be (see also Jablonski 1996, 1997, where stable, warm climates yielded body-size trends, in both passive and active modes, at roughly equal frequencies).

Hierarchical approaches to evolutionary trends were first seen in the context of punctuated equilibrium (and do seem to take on special importance for the generation of clade-level patterns when stasis is prevalent; Stanley 1979; Gould 2002), but stasis is not necessary for large-scale trends to be shaped by more than just selection and other processes at the organismic level (Bookstein *et al.* 1978, p. 133; Slatkin 1981; Sober 1984; McShea 1994; Rice 1995). When within-species anagenetic changes are significant, they can be reinforced by higher-level processes, or they may be unrelated to, or even counter to, the overall trend. To give just one classic example, the net macroevolutionary trend towards size increase in the Eocene mammal *Hyopsodus* emerges from an underlying dynamic containing three gradual size increases, one punctuational size increase, one period of size stasis and three gradual size decreases, i.e. gradualistic change was random with respect to the macroevolutionary outcome (Bookstein *et al.* 1978, p. 133; see additional mammal and echinoid body-size changes cited by Jablonski 1996, p. 273).

Trends driven by directional speciation, emphasized by Hallam (1978, 1998) among others, pose a different sort of question: does a bias in the phenotypes produced over a series of speciation events reflect only constant (or episodically consistent) selection pressures, or does it also reflect an intrinsic, developmental component? We know that not all developmentally feasible phenotypes are equally probable (e.g. Arthur 2002, 2004; Gould 2002; Hansen and Houle 2004; Brakefield 2006), and that on very broad scales morphological convergence and iteration occurs frequently (e.g. Vermeij 2006), but we do not know whether developmentally biased generation of morphologies has actually generated stepwise evolutionary trends, either directly or indirectly via hitch-hiking effects.

A first step might be to test for congruencies between the phenotypic variance-covariance structure within and among species, and the direction of large-scale trends that arise from those species (as found in an ostracode lineage by Hunt 2002; see also Hansen and Martins 1996; Schluter 2000); such tests address only one of several possible ways that developmental factors might condition macroevolutionary patterns, however.

Trends and other macroevolutionary patterns might also be shaped by ecological interactions. Sometimes, as with the escalation of durophagous predation through the Mesozoic and Cenozoic, large-scale trends do appear to reflect upward-cascading effects from the organismic level (see Vermeij 1987; Aronson 1994). However, more complex cross-level dynamics can also occur, as when predation or competition, which by definition negatively affect species at the organismic and population level, fragment populations or otherwise impose pressures that actually promote speciation or diversification rates (e.g. Stanley 1986; Schluter 2000; Nosil and Crespi 2006). We need more sophisticated models for the macroevolutionary roles of biotic interactions (see discussions in Sepkoski 1996; Jablonski in press), and for the dynamics of species in meta-communities, where multiple habitat patches are linked by dispersal so that, for example, species that occur together fail to interact in a continuous or consistent fashion (McPeck 2007; see Benton and Emerson 2007 for a different, and more extrapolationist, viewpoint).

With so many processes operating on clades simultaneously at multiple levels, most workers have logically sought examples where processes at one level overwhelm those at other levels or where one type of passive or active dynamic greatly predominates. However, most clades probably experience more complex pressures, and those may change over geological time-scales. The relative contribution of different mechanisms to shaping a given trend can be assessed in several ways. For example, partitioning skewness in the distribution of the trending character among and within subclades can quantify the active and passive components of a trend (Wang 2001). Attempts to address multilevel processes by expanding Price's covariance selection equations (Damuth and Heisler 1988; Arnold and Fristrup 1992; Okasha 2004; Rice 2004) have found few applications, but likelihood approaches may be more successful, for example, in testing the association of differential speciation or extinction rates as opposed to anagenetic change or directional speciation, with the net morphological trend of a clade. Such approaches have been little explored and will face difficulties pinpointing the focal level of selection, but are likely to produce novel insights (see Wagner 1996; especially C. Simpson, pers. comm. 2006 for pioneering work).

ORIGIN OF NOVELTIES

The origins of major novelties and higher taxa need to be evaluated in terms of *both* scale and hierarchy. The fossil record shows strong temporal and spatial patterns that violate expectations derived by simply scaling up simple random-mutation models to the origin of major groups or new body plans. We have known since the path-finding work of Valentine (1969, 1973) about the strong discordances between the first appearances of higher taxa and diversity dynamics at the species or genus level: every new clade of high rank must begin with a new species, but when and where those clade-founding species occur evidently depends strongly on ecological context. [The use of higher taxa as proxies for major novelties appears to be relatively robust for many animal groups (e.g. Bambach 1985; see Jablonski 2005*b* and references therein; and Erwin 2007) but less effective in plants, where higher taxa are based on reproductive structures rather than remodelling of body plans.] Concerns that such temporal patterns are simply inevitable artefacts of the branching topology of evolutionary trees (e.g. Raup 1983; Smith 1994) are allayed by the finding that clades tend to fan out in morphospace early in their histories, generally while at relatively low taxonomic diversities (see reviews by Foote 1997 and Erwin 2007, who both note some exceptions). Such evolutionary bursts in disparity relative to taxonomic diversification occur in early Palaeozoic invertebrates (Foote 1997; Thomas *et al.* 2000; Valentine 2004; Conway Morris 2006), mid-Palaeozoic land plants (Bateman *et al.* 1998; Boyce and Knoll 2002; Boyce 2005) and vertebrates (Ahlberg *et al.* 2006; Ruta *et al.* 2006), early angiosperms (Lupia 1999), and even in Proterozoic eukaryotes (Huntley *et al.* 2006; but see Butterfield 2007 for caveats).

The jury is still out on whether these pulses of evolutionary inventiveness and, just as important, the cessation of these pulses derive mainly from developmental or ecological factors, although environmental triggers and ecological feedbacks are currently in favour (e.g. Valentine 1995, 2004; Knoll and Carroll 1999; Ciampaglio 2002, 2004; Erwin 2005, 2007; Peterson *et al.* 2005; but for a blurring of the need for 'either/or' arguments, see Webster 2005; Marshall 2006). Definitive tests have been difficult to frame, in part because we still have a window on only a fraction of the developmental mechanisms involved in these radiations, and even attempts to use the less profound episodes of evolutionary innovation seen in the wake of mass extinctions as vehicles for testing the rival hypotheses have been indecisive (e.g. see Erwin *et al.* 1987 and Ciampaglio 2004 vs. Foote 1999 for contrasting interpretations of the early Mesozoic recovery from the end-Palaeozoic extinction). We cannot rule out the rather

daunting possibility that the truth incorporates both views. Ecological context is almost certainly essential to the story, and the basic gene-regulatory machinery was clearly in place well before the Cambrian diversification of animals (reviewed by Valentine 2004; Erwin 2005; Peterson *et al.* 2005; it was similarly in place before the diversification of land plants, not to mention angiosperms; see Nam *et al.* 2003; Friedman *et al.* 2004; Tanabe *et al.* 2005), but we still know little about how gene networks are actually repatterned or redeployed, or the long-term role, if any, of 'genetic lines of least resistance' (Schluter 2000) that appear to arise in the short term. Other kinds of intrinsic factors may also come into play. For example, Niklas's (1994, 2004) models suggest that a shift from selection focused mainly on a single function to selection for the simultaneous performance of many functions (as might be expected in the wake of a functional breakthrough, as when vascular plants solved the water-conservation problem) will unleash diversification because many different trait combinations can have similar relative fitnesses (see also Marks and Lechowicz 2006, and Marshall 2006 for application of this approach to the Cambrian explosion).

We are beginning to understand the developmental basis for the origin of novel morphologies (with a steady stream of books and symposia in this area, including Müller and Newman 2003; West-Eberhard 2003; Pigliucci and Preston 2004; Schlosser and Wagner 2004; Valentine 2004; Carroll *et al.* 2005; Hallgrímsson and Hall 2005). It is clear that the organization of gene regulation allows for more coordinated and repetitive phenotypic changes than was expected from genetics based strictly on the coding sequences of equal and small effect, embedded in a web of seemingly random pleiotropy. However, we still have little idea of how interclade differences in developmental systems can affect macroevolutionary dynamics. Important factors might include (among many others, drawing on the books cited above): the topology of gene networks and the way they interlock; mechanisms for modulating multiple gene expression events (e.g. via duplicate genes free to diverge in function vs. the accumulation of regulatory switches associated with single gene copies); how a body is partitioned into developmental modules at the molecular, cellular, tissue and organ levels; the extent and nature of phenotypic plasticity, i.e. the battery of phenotypes that can be environmentally invoked from a single genotype; and the variety and power of epigenetic mechanisms that integrate developing bodies to accommodate localized changes in the timing, location or intensity of developmental processes. These will be exciting times, provided that developmental research continues to feed back into the major evolutionary questions. and as discussed in the preceding paragraph, all of these developmental processes occur within an environmental context

that feeds back on development in complex ways, so that the field currently dubbed 'evo-devo' needs to evolve into 'eco-evo-devo' (see Wake 2004; Jablonski 2000, 2005b).

Not all evolutionary novelties meet with immediate success or have immediate ecological impact. Macroevolutionary lags, where origination of a major group or acquisition of a major innovation is followed by a long quiet phase before an upturn in diversity or abundance (Jablonski and Bottjer 1990; Jackson and Erwin 2006), are quite common in the geological record. Many of these lags, such as the delay between the origin of mammals and birds and their Cenozoic heyday, almost certainly reflect priority or incumbency effects (Jablonski and Sepkoski 1996). The end-Cretaceous extinction of various archosaur clades opened up a host of ecological opportunities, the argument goes, and dramatic diversifications ensued. This is not to say that birds and mammals were completely static during the Mesozoic (e.g. Chiappe and Dyke 2002; Fountaine *et al.* 2005; Luo and Wible 2005), but their Cenozoic diversification is on an entirely different scale, functionally and morphologically, from their earlier gains.

Other macroevolutionary lags are probably more directly tied to physical environmental changes. For example, grasses originated in the Late Cretaceous or early Cenozoic (Crepet and Feldman 1991), diversified taxonomically by the late Eocene or early Oligocene, and finally gained ecological dominance in North America in the late Oligocene or early Miocene (Kellogg 2000; Strömberg 2005). Here we see both kinds of lags: a phylogenetic lag from origin to diversification (with the upturn associated with the end-Cretaceous event?), and an ecological lag from diversification to dominance (with the upturn associated with the aridification of central North America?). Similarly, compound lags may represent the differential impact of clade-defining novelties and the later acquisition of traits that directly boost diversification rates. For example, the cheilostome bryozoans first appeared in the late Jurassic, expanded environmentally at low densities and diversities through the latest Jurassic and most of the early Cretaceous, then exploded morphologically, functionally and in terms of biomass in the mid-Cretaceous around the time they acquired brooded, low-dispersal (and speciation-promoting) larval development (Taylor 1988; Jablonski *et al.* 1997). These discordances among different measures of evolutionary success attest to the value of tracking not just diversity but abundance in macroevolutionary dynamics (McKinney *et al.* 1998, 2001; Jackson and Erwin 2006).

Environmental patterns in the origins of higher taxa are also recorded on Phanerozoic time-scales. Higher taxa of benthic marine invertebrates preferentially originated in onshore, disturbed habitats, at least over the past 250 myr. This pattern holds even for clades that today

occur at all depths, or are restricted to offshore settings, so that present distribution is not a reliable indicator of evolutionary origins. By contrast, at lower hierarchical levels the first appearance of genera appears to be diversity-dependent, shaped by clade-specific bathymetric gradients. These results appear to be robust to sampling biases, taxonomic revisions and new discoveries, and, in the few instances tested, to the use of apomorphies or morphospace occupation rather than taxonomic proxies for the origins of novelties (Jablonski and Bottjer 1990; Eble 2000; Jablonski 2005b) (Text-fig. 5). Here is a macroevolutionary problem sitting squarely at the intersection of palaeontology, ecology and developmental biology, a site that should be fertile ground for interdisciplinary research.

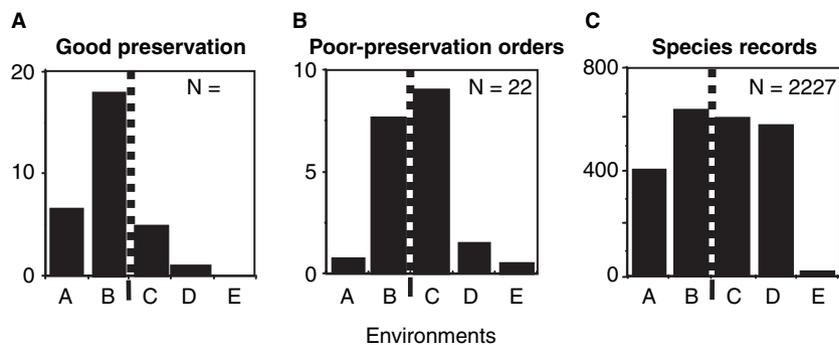
Post-Palaeozoic higher taxa also preferentially first occur in the tropics; and most of them also still occur there, thereby apparently falsifying the long-standing dichotomy portraying the tropics as a cradle or a museum (see Jablonski 1993, 2005b). The tropical origins of most major groups also appears to be robust to sampling and taxonomic treatment (the bias towards better sampling in temperate latitudes should generate the opposite pattern; see Jablonski 1993; Valentine *et al.* 2006), but mechanisms have been little explored (but see Willig *et al.* 2003; Wiens and Donoghue 2004; Goldberg *et al.* 2005). The fact that genera also appear to originate preferentially in the tropics (Jablonski *et al.* 2006 and references therein) might suggest that this dynamic prevails at all levels, but we simply lack the data to test whether the origins of higher taxa or major novelties occur at a higher *per-taxon* rate than in higher latitudes. The counter-intuitive latitudinal shift of species/genus ratios within clades (with tropical clades having *lower* ratios in marine molluscs; Roy *et al.* 1996a), and the failure of bathymetric trends to track across levels, suggests more complex hierarchical effects, but this is virtually unexplored. Similarly,

the relation between major morphological innovations and subsequent functional diversifications, as established clades explore new ways of making a living, has received relatively little attention (see Bambach *et al.* 2007 for a valuable step in this direction).

EXTINCTIONS

Losses

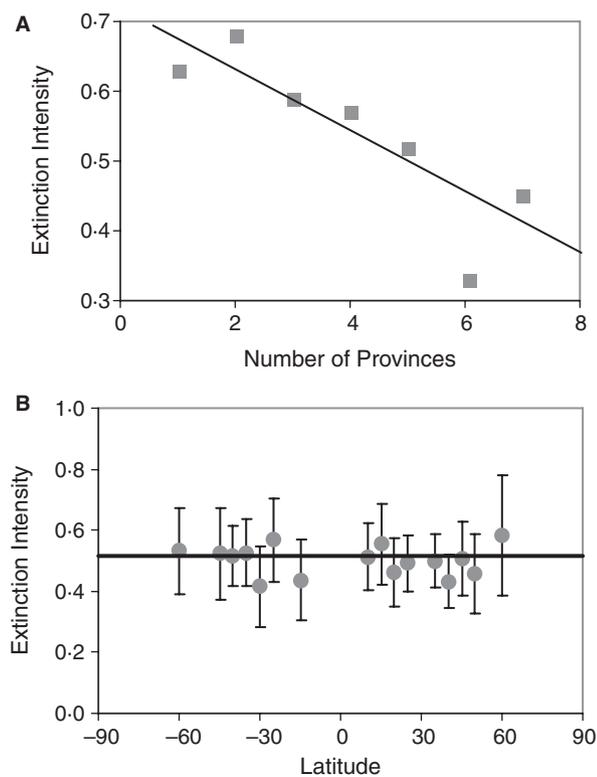
Scale and hierarchy also both come into play when considering the evolutionary role of mass extinctions. Expanding the temporal scale of extinction time-series to encompass the entire Phanerozoic, we see several episodes of extreme extinction intensity (see Jablonski 2005a for a discussion of the side issue of whether the major mass extinctions constitute a separate class of extinction intensities). However, mass extinctions are important to macroevolution not only because they involve a sharp increase in extinction intensity over immediate 'background' levels but also because they evidently can bring a change in extinction selectivity. Many of the traits demonstrably associated with reduced extinction rates during 'normal' times appear to be ineffective during one or more mass extinctions (reviewed by Jablonski 2005a). These factors include body size, local abundance, reproductive mode, feeding strategy and other aspects of life habit, and, at the clade level, geographical range of constituent species and species richness. On the other hand, broad geographical range at the clade level promotes taxon survivorship for at least some marine groups during each of the 'Big Five' mass extinctions (see Jablonski 2005a, table 1). For end-Cretaceous bivalves, which have received the most detailed study, this benefit of broad geographical range at the genus level is not simply reducible to increasing probability of encountering a



TEXT-FIG. 5. Environments of first occurrence in post-Palaeozoic marine invertebrate taxa. A, good-preservation groups differ significantly from B, poor-preservation groups and C, the distribution of species occurrences within good-preservation orders of crinoids, echinoids and cheilostome bryozoans, counting every record of a species as an occurrence. Onshore environments: A, nearshore; B, inner shelf. Offshore environments: C, middle shelf; D, outer shelf; E, slope and deep basin. (After Jablonski 2005b.)

low-extinction refuge, at least at the province scale. Extinction intensities are statistically indistinguishable among all 16 Late Cretaceous provinces (Text-fig. 6).

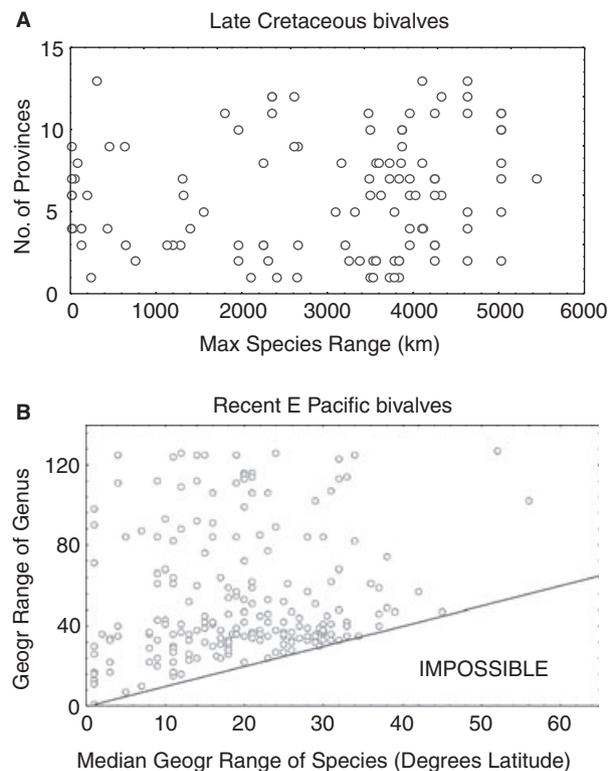
Another potential non-hierarchical mechanism for the preferential survival of widespread genera might be that such genera consist mainly of environmentally tolerant, ecologically successful or generalized species that also had broad geographical ranges. However, for end-Cretaceous bivalves and gastropods, genus survivorship is unrelated to median (Jablonski 1986*b*) or maximum geographical range at the species level within North America (where sampling at this scale is strongest) (Jablonski, unpublished). In a more general test of cross-level relationships, geographical range at the species level within North America is unrelated to province-level geographical range in Late Cretaceous bivalves (Text-fig. 7A), and geographical range along the eastern Pacific shelf of present-day bivalve species is unrelated to the geographical range of their genera (Text-fig. 7B) (Jablonski 2005*a*). Ecological tolerances, dispersal ability and other properties of con-



TEXT-FIG. 6. A, significant inverse relation between geographical range (as measured by number of biographic provinces occupied) and extinction intensity in marine bivalves for the end-Cretaceous extinction (after Jablonski and Raup 1995). B, for marine bivalve genera, extinction intensities are indistinguishable among Late Cretaceous biogeographical provinces, indicating that province-scale refugia cannot explain the preferential survival of widespread genera. Error bars are 95 per cent binomial confidence intervals.

stituent species must play some role, but too many other factors are involved in determining clade-level geographical range for simple extrapolation from organismic traits to apply. By the criteria outlined above, geographical range is thus an emergent property at the clade level as well. However, in contrast to the species level, clade geographical range is probably not heritable, so that the selectivity of mass extinctions will not be cumulative; as with any non-heritable trait, we can have selection but no potential for evolution.

On the other hand, loss or severe reduction of taxa, morphospace occupation, or functional variety could occur as indirect effects stemming from correlations with other selective targets such as geographical range.



TEXT-FIG. 7. Geographical range at the genus level is unrelated to the maximum geographical range of their constituent species in A, Late Cretaceous marine bivalves and B, present-day bivalves of the eastern Pacific shelf. In A, species-level range is measured in km along the Upper Cretaceous outcrop of the Gulf and Atlantic coastal plain and genus-level geographical range is measured by number of biogeographical provinces occupied ($n = 113$ genera, $r = 0.13$, $P = 0.16$; a similar result is seen if median geographical range of species is used). In B, geographical range is measured in terms of degrees latitude; the lower right corner of the graph represents a field of impossible combinations: species cannot be more widespread than their genera ($n = 213$ genera, $r = 0.17$, $P = 0.81$; statistical significance was assessed by resampling the data, using 10,000 repetitions where impossible combinations were discarded with replacement) (after Jablonski 2005*a*).

Consider some of the organismic traits that suffered during mass extinctions: broad apertural sinuses in snails, multiple stipes in graptolites, complex sutures in cephalopods, elongate rostra in echinoids, schizodont and pachyodont hinges in bivalves (Jablonski 2005a). It is difficult to believe that these phenotypes were *directly* selected against during mass extinction events. However, we have many clear instances when more morphological, functional or higher-taxonomic diversity is lost than expected from purely random species removal (e.g. Roy 1996; Foote 1997, 1999; McGhee 1999; McGowan 2004a, b; Allen 2006), and those losses had long-term evolutionary consequences for their clades. More work is needed to segregate direct selectivities from such hitch-hiking effects during mass extinctions; and indirect effects can be even more complex if ecological interactions come into play (e.g. the apparent preferential survival of wind-pollinated plants at the K/T boundary, which might ultimately derive from selectivity in insect extinction rather than direct environmental effects on the plants; Sweet and Braman 1992, 2001). Given the potential for complex, multi-level interaction effects, multivariate approaches such as those discussed above (Text-fig. 3) seem the best way forward. It is worth keeping in mind that if mass-extinction survivorship is simply indifferent, rather than truly antithetical, to many of the factors that promote success during the normal times that constitute the vast bulk of geological time, then some 'preadaptation' to mass extinction drivers should occur by chance (see discussion by Jablonski 2005a).

Recoveries

I have already mentioned the association of evolutionary bursts with recoveries from mass extinctions. Dramatic evolutionary divergences or high rates of apomorphy acquisition tend to be more clearly concentrated in initial radiations than in recoveries, but this needs more thorough analysis, and some authors have reported post-extinction increases in the amount of morphological divergence per branch-point (Anstey and Pachut 1995; Wagner 1995, 1997; Foote 1999; Eble 2000; for general reviews, see Erwin 2001, 2004; Jablonski 2001, 2005a). Studies of this kind will be especially valuable when they include cross-level comparisons, as in Patzkowski's (1995) finding that bivalves and mammals produce more new genera relative to estimated speciation rates during post-extinction recoveries than expected from 'normal' times.

More puzzling are the clades that survive mass extinctions but fail to participate in the evolutionary recovery. Just as survivors of mass extinctions can be difficult to predict from pre-extinction successes, long-term post-extinction successes are difficult to predict from the

survivors of mass extinctions. Recoveries need not involve an across-the-board expansion of a surviving clade in morphospace, but can instead involve only subregions of the occupied morphospace or be channelled in just one or a few directions (e.g. Dommergues *et al.* 1996, 2001; Lockwood 2004, 2005; McGowan 2004a, b, 2005; Allen 2006; Erwin 2007). In extreme cases, taxa can weather a mass extinction only to disappear a few million years later, or fall into marginal roles. A simple probabilistic model would treat post-extinction success as a function of the severity of the clade's bottleneck at the boundary, with the expectation that the probability of avoiding stochastic extinction or marginalization in the post-extinction world should be positively related to the number of surviving subtaxa within the clade. However, this model has failed several empirical tests (Jablonski 2002). As already noted, clade interactions must also be an important component of macroevolution, if only from the standpoint of priority or incumbency effects that presumably dampen diversification dynamics under many circumstances.

Recovery dynamics are poorly understood, in part because they have received so little attention from a comparative standpoint. Presumably, as with any large-scale biotic upheaval, the post-extinction trajectories of clades depend upon the interaction of intrinsic diversification rates (as set by organismic and higher-level traits), biotic interactions and physical environmental factors, along with stochastic effects. But much more work is needed before we have a general theory for the interplay of these factors, particularly for recoveries. For example, the relative role of the aforementioned factors might plausibly vary with extinction intensity, with the spatial extent of the perturbation that drives the extinction, or with the biogeographical context of the focal clade, but few data can verify that. More detailed comparisons of diversification during 'normal' and post-extinction intervals are also needed to determine how far recovery intervals actually do diverge in their dynamics from the bulk of geological time (e.g. Jablonski 2005a; Harnik and Simpson 2006), and recovery dynamics at different hierarchical levels and in terms of different biological metrics (taxonomic, morphological or functional diversity) are just beginning to be explored. Comparative, multivariable analyses of evolutionary recoveries will surely be a fruitful research direction.

CONCLUSIONS

Macroevolution is the most history-based wing of evolutionary biology, which makes it particularly challenging and multidisciplinary. Historical context and the biological raw material available to a clade must be important to

many aspects of macroevolution, and I have barely touched upon those aspects here. But it is clear that selection pressures favouring flight have not reliably produced birds. Bats, pterosaurs, a host of gliding forms from snakes to squirrels, and hordes of arthropods from butterflies to parachuting spiders have taken to the air at different times and on different branches of the metazoan tree; the number of species varies by several orders of magnitude among those groups, and not all of them are still with us. These large-scale patterns fall into the domain of macroevolution. Despite the contingent aspects of these historical events, the history of life and the deployment of biodiversity today do not simply represent massive stochasticity layered on top of selection among millions of infinitesimally small mutations in millions of bodies in millions of species over billions of years. They involve a set of dynamics also operating above and below the familiar level of bodies within populations, with rules manifested as statistical patterns in morphospace and the differential waxing and waning of clade richness. The macroevolutionary principles reviewed here in no way invalidate the operation of the traditional neodarwinian mechanisms, but they expand evolutionary theory to a richer and more realistic picture of processes across a range of temporal and spatial scales and across hierarchical levels.

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