

Evolutionary macroecology and the fossil record

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Introduction

From the very outset of the recent burst of work in macroecology it has been clear that major macroecological patterns have a strong historical underpinning. Many spatial relationships bear the imprint of Pleistocene climatic changes, and patterns underlain by differential speciation and extinction have their roots even deeper in geological time. Although efforts to infer long-term dynamics from the topology of phylogenetic trees are increasing, many macroecological analyses inevitably yield only static snapshots of biotic patterns. The fossil record offers a rich archive of natural experiments in the *dynamic* relationships among many of the variables of interest to macroecologists, including how those variables respond to perturbations of all magnitudes. Thanks to the temporal scope and thus range of phenomena encompassed by the fossil record, these perturbations range from modest temperature changes to extreme glacial–interglacial cycles, and from subtle shifts in productivity that track long-term changes in the carbon cycle to sudden upheavals triggered by the impact of objects 10 km in diameter. Thus, although as with any large and heterogeneous database care must be taken to avoid sampling and other artefacts, palaeontology can provide direct empirical data on the dynamics underlying macroecological patterns: spatial shifts, origination, extinction and trends over spans of 10^3 to 10^7 years (see also Clarke & Crame, this volume). At the same time, palaeontologists need to incorporate macroecological insights into their research, particularly regarding the linkage and covariation found among the important variables (Lawton 1999; Gaston & Blackburn 2000; Blackburn & Gaston 2001).

Spatially explicit palaeobiological research has been somewhat neglected in favour of synoptic, global-scale analyses, but a growing body of palaeobiological work with a strong spatial component is a welcome development that will further promote the integration of disciplines into what might be termed evolutionary macroecology.

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Targets for palaeobiological analysis have included, among others: the relationship between intrinsic biological traits and geographical distributions as well as durations of taxa (reviewed e.g. by Stanley 1979, 1990; Jablonski 1995; McKinney 1997a,b; Kammer *et al.* 1998); the shape and dynamics of body-size distributions (Jablonski 1996, 1997; Alroy 1998; Roy *et al.* 2001a); the packing of species and higher taxa into regions and provinces, through time and along gradients of latitude, longitude and depth (Valentine 1973; Valentine *et al.* 1978; Stanley 1979; Sepkoski 1991; Jablonski 1993); and ecological responses to changes in the physical environment, in resource availability, and in biotic interactions (reviews by Vermeij 1994; Jablonski 1995, 2001, 2002; Jablonski & Sepkoski 1996; Miller 1998; Erwin 2001).

Marine macroecology, an essential bridge to the fossil record

Palaeontologists have studied macroecological aspects of the fossil record for decades, just as some ecologists did macroecology long before the term was introduced (see Lawton 1999). The richness and density of the marine fossil record has promoted a predominantly marine invertebrate approach to evolutionary macroecology. Certainly, there are a number of important studies in the evolutionary macroecology of terrestrial organisms. However, owing to sampling and other obstacles, these studies are restricted mainly to North American and European mammals, plants and insects. Forging stronger ties between palaeobiology and ecology on one hand, and establishing the generality of macroecological 'rules' on the other, will clearly require a serious effort in the macroecology of the modern marine biota.

Gaston & Blackburn (1999, p. 355) list a set of variables important to macroecology, including 'species richness, abundance, range size, body size, trophic or functional group, life history, and reproductive traits'. Interrelationships among some of these variables, such as abundance, geographical range and body size, have been a central focus of terrestrial macroecology. These variables are still not well known for marine organisms (e.g. Chapman 1999), nor have their interactions been much addressed in palaeobiological analyses. However, the compilation of distributional data and a number of other key variables is proceeding for major groups.

Marine and terrestrial environments differ profoundly in terms of key biotic and abiotic processes, ranging from patterns of primary productivity to structures of food webs to modes of dispersal and aspects of life histories (Clarke 1993; Steele *et al.* 1993; Cohen 1994; Roughgarden *et al.* 1994). One of the most intriguing research agendas is simply to test whether these differences in processes lead to different macroecological patterns in the sea. For example, the reproductive strategies of most marine invertebrates select for life histories that differ in many respects from those of the land vertebrates. Dispersal tends to be more extensive, and dispersal stages much more abundant, in marine invertebrates (e.g. Strathmann 1990). Further, fecundity usually scales positively with body size rather than negatively as in birds and mammals, a contrast that may be important in understanding patterns in size–frequency distributions and the role of body size in invasion success (e.g. Roy *et al.* 2000a, 2001b).

Body size

It has become a cliché that body size affects almost every aspect of the biology of a species, from physiology to life history, and that it plays an important role in the organization of ecological communities. Here we address only two aspects of body size in the marine fossil record: its relation to the volatility of geographical ranges in response to changing climates and other perturbations, and the behaviour of clades relative to modal body sizes over geological timescales.

Range expansions

The west coast of North America contains one of the world's best-studied Pleistocene (Valentine 1961, 1989) and Recent molluscan faunas (see Roy *et al.* 2001a, 2002). Comparisons of Pleistocene and modern distributions of these species have shown that the range limits of many of these taxa shifted significantly in response to past climatic changes (both warming and cooling). Body size appears to have played an important role in mediating the responses of these molluscan species to climate change. The extralimital species, as a group, have significantly larger body sizes than the rest of the Pleistocene species pool (Roy *et al.* 2001b; Fig. 19.1). Interestingly, the same size bias is also seen in marine bivalve species with geographical ranges that have expanded in historical times thorough human-mediated introductions (Roy *et al.* 2001b). In the latter case, the selectivity is evident for regional assemblages and in a global analysis of the mussels (Family Mytilidae), chosen because it is the clade with the greatest number of (non-commercial) invasive species (Roy *et al.* 2002) (Fig. 19.2). Among the invasive bivalves of the temperate northeastern Pacific coast, large invasive species are also significantly more widespread in their new ranges compared with small ones (Roy *et al.* 2002). Finally, on a geological timescale, large-bodied bivalve genera predominated in biotic interchanges following the end-Cretaceous (K–T) mass extinction, 65 million years ago (Ma). The K–T event was one of the large five mass extinctions of the Phanerozoic, and although extinction intensities were surprisingly homogeneous worldwide, the recovery, which lasted several million years at least, differed among continents (Jablonski 1998). The faunal recovery in the Gulf Coast of the USA was more strongly driven by invading species than in the other regions. As shown in Fig. 19.3, the post-Cretaceous invaders in the Gulf Coast are significantly larger than the taxa indigenous to the region. Although the data in this last example are at the generic level, the patterns match those in the Pleistocene and Recent examples.

All of these observations together suggest that range limits of large-bodied marine bivalves tend to be more volatile compared with those of smaller species. These patterns are different from terrestrial case studies, involving birds and mammals, where no consistent relationship between body size and invasion success has emerged (Veltman *et al.* 1996; Forsy & Allen 1999; Duncan *et al.* 2001). One hypothesis for this contrast between bivalves and higher vertebrates is that the difference derives from the positive relationship between body size and fecundity in marine bivalves, as opposed to the negative relationship seen for interspecific comparisons in mammals and birds (Roy *et al.* 2002). The difference is seen even when larval

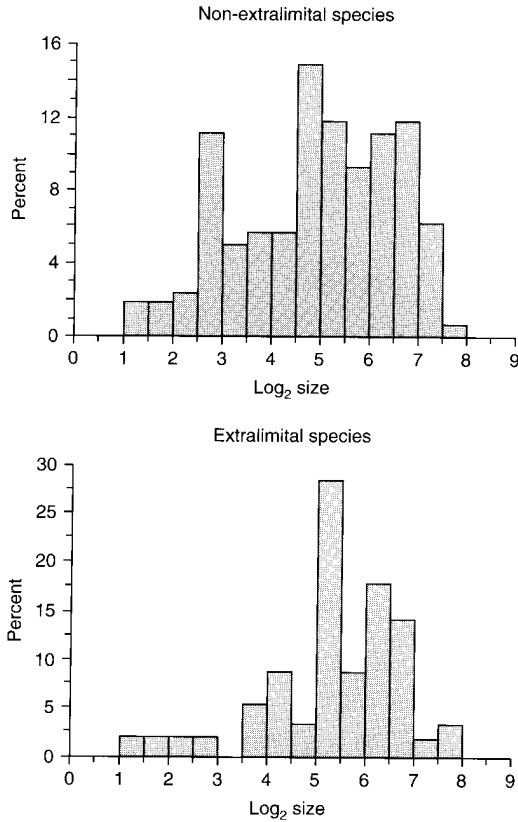


Figure 19.1 Size–frequency distributions of species with Pleistocene occurrences that do not fall outside their present-day range (top; $n = 160$), compared with species known to have occurred at least 1° latitude outside their present-day range limits during the Pleistocene (bottom; $n = 56$). The extralimital species are significantly larger in size (body size is taken as the geometric mean of length and height (mm); size data \log_2 -transformed before analysis; $p < 0.01$, Mann-Whitney U test). (After Roy *et al.* 2001b.)

mode, and thus dispersal ability, is held constant (Roy *et al.* 2002). In any event, the concordance of modern, Pleistocene and Cretaceous results, despite the very different sampling issues, different modes of transport and different kinds of perturbations in the recipient provinces, suggest a general rule relating invasiveness to body size for marine bivalves, but one that may not be applicable to terrestrial vertebrates.

Body size evolution

The fossil record permits us to track the evolutionary dynamics underlying macroecological patterns in body size, which have been quite controversial (see reviews by Jablonski 1996; Gaston & Blackburn 2000), and holds some surprises.

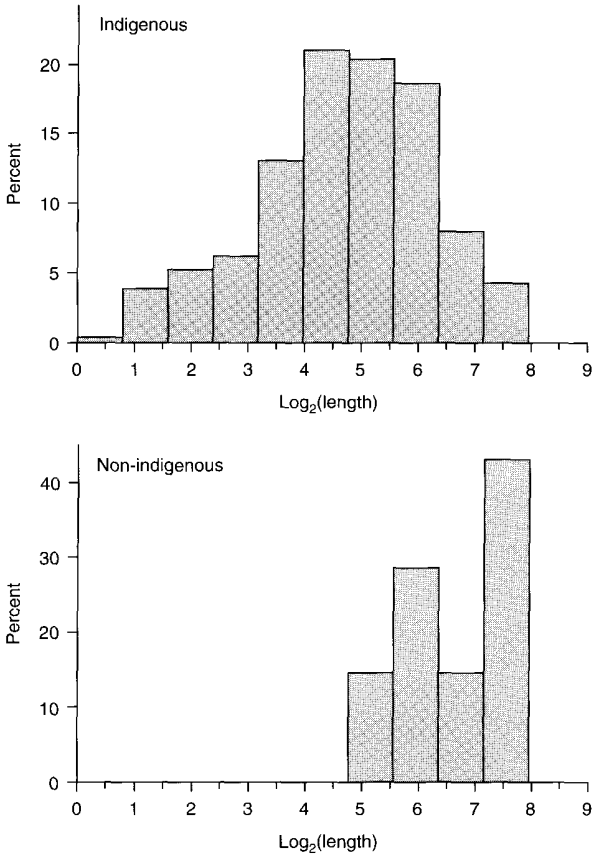


Figure 19.2 Size–frequency distributions for the intertidal and shelf–depth mytilid bivalve species of the world. Non–mariculture species that have been introduced outside their native ranges through human activity (below, $n = 7$) are significantly larger than the species not known to occur outside their native ranges (indigenous species, above, $n = 292$); $p = 0.0001$, Mann–Whitney U test. (After Roy *et al.* 2002.)

Roy *et al.* (2000a) found remarkable constancy of body size distributions over four biotic provinces arrayed along the northeastern Pacific shelf from the Equator to the Arctic Ocean, despite a fourfold decrease in species richness, an almost complete turnover in species, and a considerable shift in family–level composition. A more detailed analysis revealed latitudinal trends in body size within individual provinces but no net trend from the Equator to the North Pole (Roy & Martien 2001). In addition, marine bivalve size–frequency distributions tend to be log–normal or slightly left–skewed (Roy *et al.* 2000a) as opposed to the right skew seen in most vertebrate clades (e.g. Gaston & Blackburn 2000).

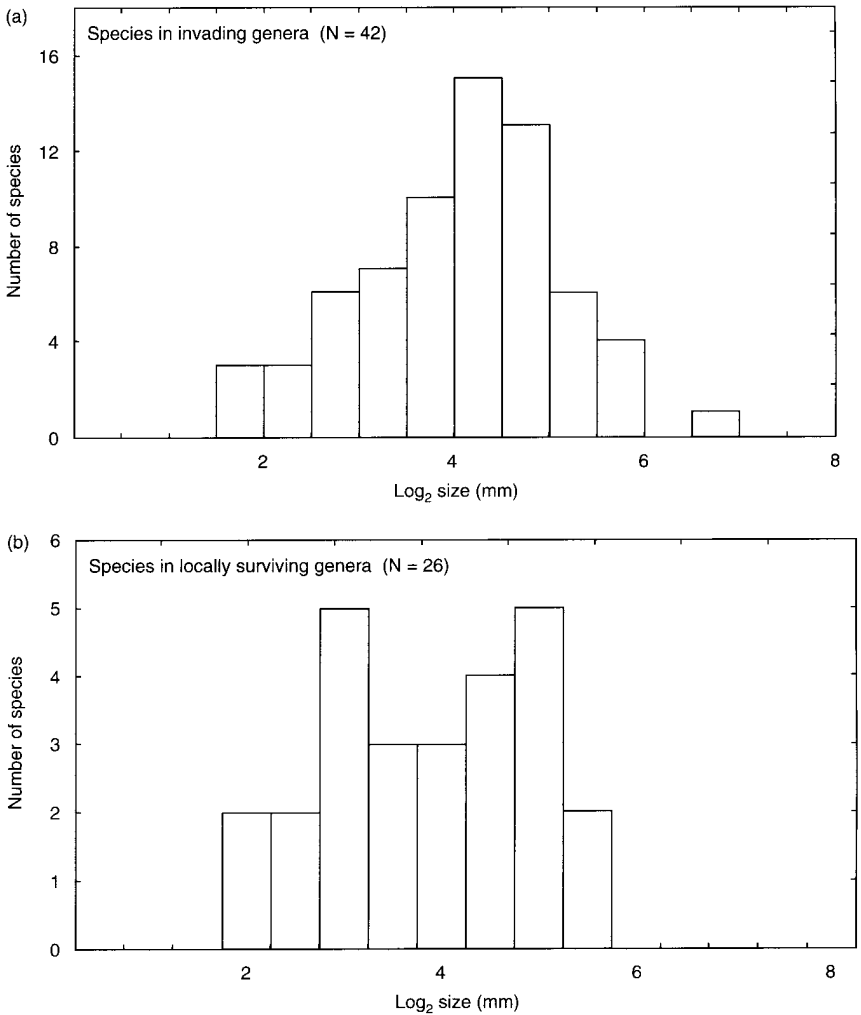


Figure 19.3 Bivalve invasions of the North American Coastal Plain province after the end-Cretaceous mass extinction were size-selective. Species belonging to genera that invaded the province (a) were significantly larger than species belonging to genera that survived locally (b) ($p = 0.02$, Mann–Whitney U test).

The energetic model of Brown *et al.* (1993), developed for mammalian faunas, successfully predicts the modal size of the northeastern Pacific bivalve distributions, thereby suggesting a role of energetics in the evolution of marine bivalve size distributions (Roy *et al.* 2000a). However, despite the stability of the body-size mode over four provinces spanning more than 75 degrees of latitude, the fossil record provides no evidence that the mode operates as an evolutionary attractor (Roy *et al.* 2000a). A

more realistic alternative, that the mode is indeed a clade-wide optimum but entry is generally blocked by established species (e.g. Maurer *et al.* 1992; Brown 1995), is also undermined by the palaeontological evidence for the highly dynamic behaviour of bivalve lineages relative to the modal size (Fig. 19.4). The failure of these molluscan lineages to exhibit any kind of organized dynamics relative to the mode suggests that the temporal and spatial constancy of that mode involves species sorting, that is differential origination and extinction within and among size classes, rather than directional trends in individual lineages (Roy *et al.* 2000a). Again, speciation and extinction rates operating over millions of years are implicated in the shaping of macroecological patterns.

Geographical range and evolutionary dynamics

The relationship between geographical range size and evolutionary dynamics—speciation rates, extinction rates and species durations—figures into many macroecological models and analyses (for reviews see Chown 1997; Gaston & Chown 1999; Gaston & Blackburn 2000; Hubbell 2001). Palaeontological data can be used to test these relationships directly, in systems where sampling and preservation are unlikely to overwhelm the biological signal.

Extinction

An inverse relationship between geographical range and extinction rate, or a positive relationship between geographical range and species duration, has been documented in a number of fossil molluscan assemblages (Jackson 1974; Hansen 1978, 1982; Stanley 1979; Jablonski 1986a, 1987, 1995; see also McKinney 1997a; Gaston & Blackburn 2000, p. 120), and is also generally supported by ecological data and theory (e.g. Maurer & Nott 1998; Gaston & Blackburn 2000, p. 174, and references therein). Analysis of a revised and updated data set for the Late Cretaceous gastropods of the Gulf and Atlantic Coastal Plain of North America shows a significant positive relationship between maximum geographical range of species at any one time and their durations in millions of years (Fig. 19.5). The geographical and stratigraphical ranges of these fossil species should not be taken as absolute values, because they are subject to incomplete sampling, but as a rank-order array of ranges and durations useful for interclade comparisons (e.g. Jablonski 1987; Jablonski & Valentine 1990). This relationship between geographical range and geological duration appears to be a general one, and in at least some situations can be shown to be robust to the kinds of sampling effects discussed by Russell & Lindberg (1988) (see Jablonski 1988; Marshall 1991; Smith 1994).

The relationship between geographical range and extinction-resistance at the species level should be viewed separately from related patterns at the clade level. However, during times of background extinction the duration of a genus is directly related to the geographical ranges of its constituent species (and this interacts positively with species richness of the genus; Jablonski 1986b). During the end-Cretaceous mass extinction, this positive effect across hierarchical levels from species to clade survival is disrupted, and survivorship is promoted instead by

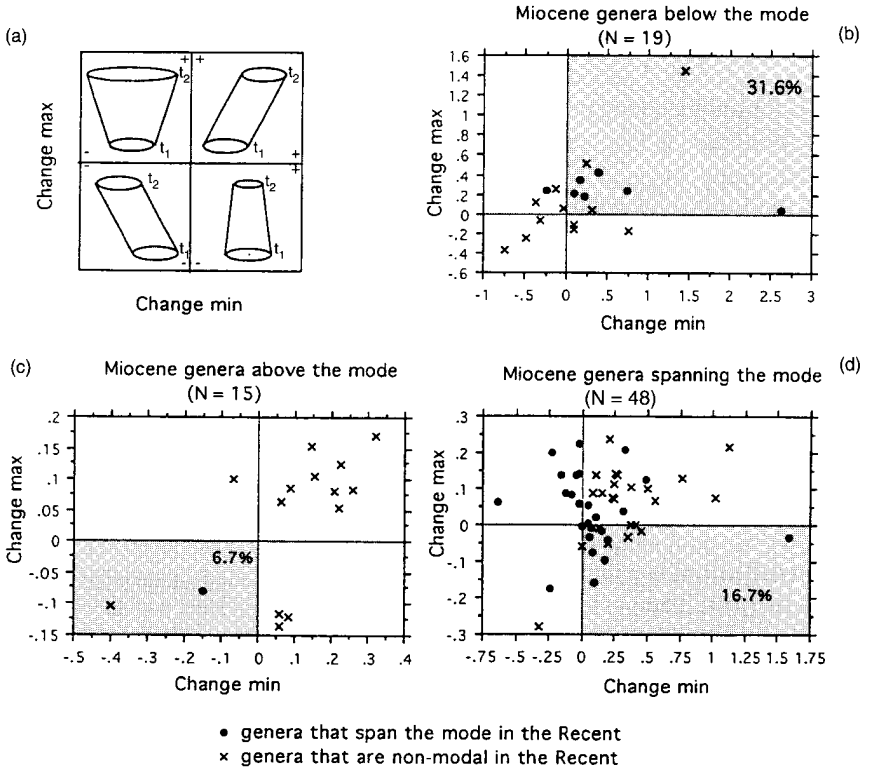


Figure 19.4 Body size evolution in Miocene–Recent bivalve genera. (a) Graphical model for body-size evolution, with each quadrant representing a different evolutionary pattern; as in Jablonski (1987), the vertical axis is the change in the upper bound of the size distribution of the species in a lineage and the horizontal axis is the change in the lower size bound of the distribution. (b–d) Evolutionary size change in 82 Miocene–Recent genera and subgenera of eastern Pacific bivalves, partitioned according to their starting position relative to the modal size; for each plot, the shaded quadrant is the one that would be the most heavily occupied if the modal size was an evolutionary attractor, with the proportion of genera actually falling into that quadrant. Of the genera that started *above* the mode, only 7% showed a directional trend towards it. Of the genera starting *below* the mode, 32% showed a directional shift towards the mode, but that is not significantly different from the 21% of clades that started below the mode but increased their size range by expansion in both directions. Of the larger number of clades that bracketed the mode in the Miocene, only 17% narrowed their size range. An equal percentage of modal clades expanded both upper and lower bounds, and almost 50% show a directional shift *away* from the mode, with most of those actually leaving the modal size class completely. (From Roy *et al.* 2000a.)

broad geographical range at the level of the clade, regardless of the within-province geographical ranges of its species (Jablonski 1986b; Jablonski & Raup 1995). This positive relationship between survivorship and geographical range at the clade level is one of few general rules that have emerged from extensive work on the ‘Big Five’ ex-

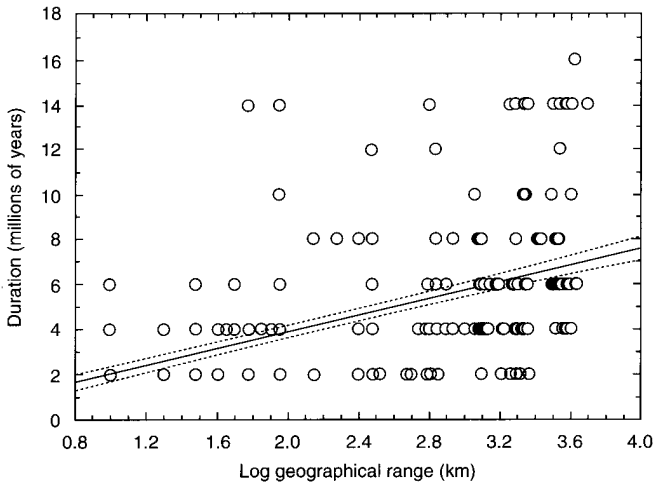


Figure 19.5 Positive relationship between geographical range and stratigraphical duration in Cretaceous gastropod species ($N = 397$). Simple linear regression, with 95% confidence interval, shown for comparative purposes (Pearson's $r = 0.62$, $p < 0.001$); a more appropriate Spearman's rank-order test is also highly significant ($R = 0.78$, $p < 0.001$).

tion events of the geological past (see Jablonski 1995, 2001). The relationship is probably also effective during background times, but is harder to detect then owing to other factors that also influence durations (Jablonski 1995).

Speciation

The relationship between geographical range and speciation rate is much more contentious. The notion of a positive relationship between geographical range and speciation rate or speciation probability is generally derived from the reasonable argument that, all other factors being equal, broad geographical ranges are most likely to be broken by barriers, leading to higher speciation rates (see Rosenzweig 1995; Chown 1997; Gaston 1998; Maurer & Nott 1998; Maurer 1999, pp. 186–189; Hubbell 2001 adopts a similar argument but emphasizes that this model probably applies most strongly to vicariant, rather than peripatric (peripheral-isolate) speciation, and Endler 1977, p. 175, applies this logic to parapatric speciation).

All other factors are rarely equal, however. As many authors have also argued, the factors that promote broad geographical ranges, such as relatively high dispersal abilities, also tend to make them relatively insensitive to barriers and thereby damp speciation rates (e.g. Mayr 1963; Jablonski 1986a; and other papers cited by Gaston & Chown 1999; see also Maurer & Nott 1998; Hubbell 2001, p. 194; Vogler & Ribera, this volume). Conversely, species with limited dispersal ability tend to have more fragmented populations that will make them more vulnerable to both vicariant and peripheral-isolate speciation (as also argued by Maurer & Nott 1998). The direct

linkages among broad geographical range, larval dispersal ability and low speciation rates have been documented in several palaeontological analyses of marine gastropods (reviewed by Jablonski & Lutz 1983; see also Hansen 1978, 1982; Jablonski 1986a, 1995; Scheltema 1989, 1992; Gili & Martinell 1994; and see Budd & Johnson (2001) on late Cenozoic corals). Although exceptions exist, the positive relationships among dispersal, gene flow and geographical range are generally well-supported for marine and terrestrial taxa (Bohonak 1999; Kittiwattanawong 1999; Pechenik 1999; Jablonski 2000; Collin 2001). There is also increasing evidence from marine taxa that species with limited dispersal capabilities tend to show more spatial structuring in phylogeographical data compared with those with high-dispersal larvae (e.g. Hellberg *et al.* 2001).

A new analysis of Late Cretaceous gastropods shows a strong inverse relation between the geographical ranges of species and speciation rate per species per million years (Jablonski & Roy 2003) (Fig. 19.6a). If this relationship is underlain by mechanisms for species cohesion such as gene flow, then, as with the extinction patterns, it is important to distinguish processes at the species level from those at the clade level (which are mingled indiscriminately by Gaston 1998; Gaston & Chown 1999; but see several species-level botanical studies with results consistent with those shown here, cited by Chown 1997, p. 97). Whatever the heritability (Jablonski 1987) or phylogenetic inertia (Harvey & Pagel 1991) between species, subdivision or budding of widespread genera may tend to give rise to more descendant genera relative to endemics. Such a relationship was found by Budd & Coates (1992) in a group of Cretaceous corals and Roy (1994) in a group of Mesozoic–Cenozoic gastropods.

We can also test whether the total number of species produced by a clade is a positive or negative function of the geographical ranges of its constituent species. Even if per-species speciation rates are lower in widespread species, it may be that the low per-species speciation rates are offset by the longer durations of their species (Gaston & Chown 1999; Gaston & Blackburn 2000, p. 119). The Cretaceous data, however, do show a weak but significant inverse relationship between geographical ranges of species and the total number of species produced by a clade (Fig. 19.6b). It is not surprising the relationship is weaker: restricted species have shorter durations, so many will die young and leave few descendants. This would yield much scatter at the left end of the plot. Wagner & Erwin (1995) analysed two Neogene clades of planktonic foraminifera and an Ordovician family of marine gastropods, with mixed results. Longer lived taxa showed some tendency to leave more descendants, but Gaston's (1998) reanalysis of the gastropods found no significant partial correlation between number of descendants and geographical range size, controlling for differences in longevity.

The palaeontological data are certainly not free of biases. Perhaps most importantly, they must lack many of the rarest species, and, depending on the spatial scale of sampling relative to the smallest viable geographical ranges, are also likely to lack some of the most spatially restricted species (Raup 1979; McKinney 1997b; Jablonski 1995; Kidwell 2001), an effect that will be accentuated if rarity and geographical range are correlated, as occurs in terrestrial organisms (e.g. Gaston &

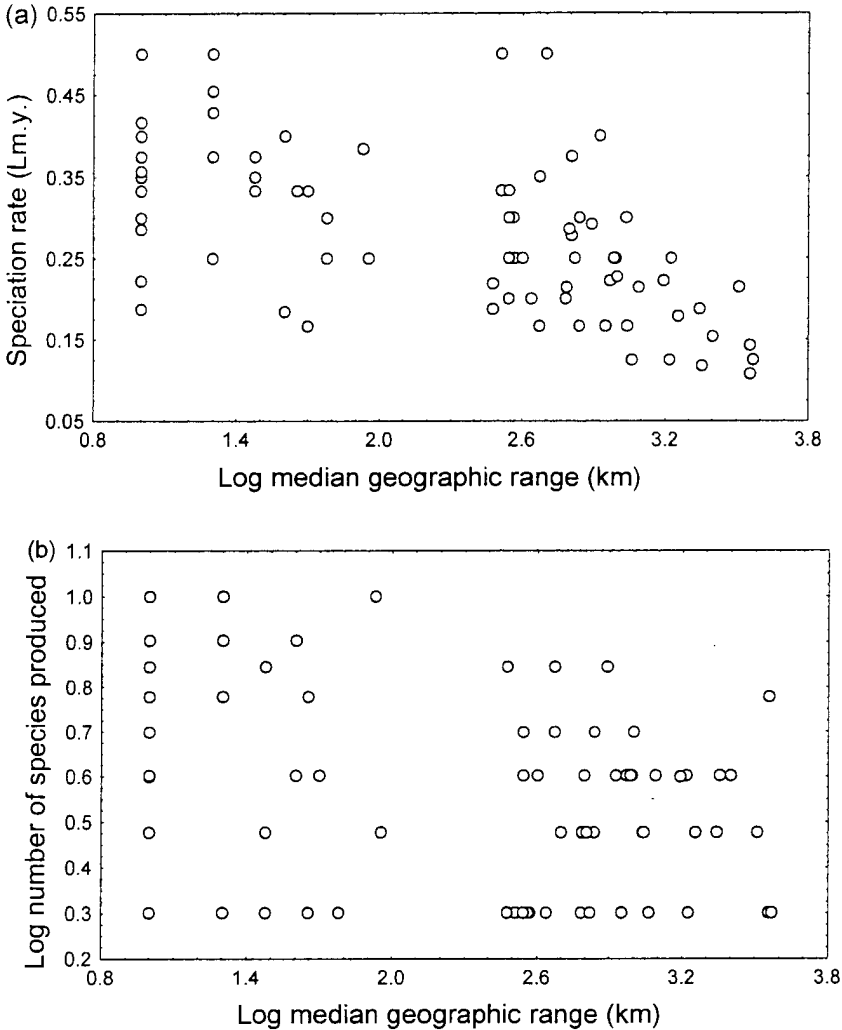


Figure 19.6 Geographical range and speciation in Cretaceous gastropods. (a) Inverse relationship between geographical range and per-species speciation rate in Cretaceous gastropods ($n = 90$ genera, Pearson's $r = -0.66$, Spearman's R for a rank-order test is -0.68 , $p < 0.00001$ for both tests); Lm.y. = per-species speciation rate in Lineage-million years (Raup 1985). (b) Weak inverse relationship between geographical range and total numbers of species produced in gastropod lineages over an 18-million-year interval of the latest Cretaceous ($n = 90$ genera, Pearson's $r = -0.24$, $p = 0.025$; Spearman's $R = -0.17$, $p = 0.10$). (After Jablonski & Roy 2003.)

Blackburn 2000) but has yet to be tested in the oceans. If these unrecorded rare species are even more ephemeral than the shortest ranging species captured by palaeontological sampling, as seems likely, this would increase their probability of disappearing before speciating. Adding them back into Fig. 19.6a would produce a downturn of the relationship between number of descendants and geographical range at the lowest ranges, giving the peaked distribution suggested by Gaston & Chown (1999).

Morphology and taxonomy through time

The fossil record provides time-series in more than just taxonomic richness and relative abundances. It permits us to analyse the *morphological* deployment of clades or communities through time. An increasingly sophisticated set of analytical methods and models have become available for the analysis of taxa within a multivariate morphospace (reviews in Foote 1996, 1997; Roy & Foote 1997; McGhee 1999; see Ciampaglio *et al.* 2001 for comparative application of different methods).

Palaeontologists applying these methods to fossil and living organisms have shown that temporal or spatial patterns of morphological diversity need not correlate with species richness, and the times and places where those two metrics of biodiversity are strongly decoupled are especially interesting. This discordance alone is sufficient to demonstrate that such analyses of morphologically defined species are not circular. More importantly, these analyses permit us directly to quantify spatial and temporal trends in specific sets of ecologically or functionally important traits. Such characters are often convergent or plesiomorphic in nature and hence not used to define individual species. For example, morphological disparity—the dispersion of taxa within a morphospace—significantly outpaced taxonomic diversity in the early Palaeozoic diversification of blastozoan echinoderms (see Foote 1996, 1997, 1999). Wills *et al.* (1994) found a similar pattern for Cambrian arthropods: the morphospace occupied by what must be a very incompletely known arthropod fauna (mainly from the Burgess Shale) was roughly equal in volume to that occupied by all living arthropod classes and subclasses, despite the vastly greater species richness and more extensive sampling today. The pattern of morphospace occupation during the intervening 500 million years is a fascinating and largely unexamined issue. Such an early burst of morphological disparity is a common pattern (see e.g. Niklas 1997; Lupia 1999; Thomas *et al.* 2000), although exceptions are known (see Foote 1997). The pattern is attributed most often to the rapid filling of a newly accessible adaptive zone, although ideas involving developmental constraints have staunch advocates (see Valentine 1995; Knoll & Carroll 1999; Valentine *et al.* 1999).

Macroecological analyses of Recent taxa have focused almost exclusively on the origin and maintenance of species richness. As a result, the relationship between macroecological processes and patterns of morphological and functional diversity is largely unknown. The application of palaeontological methods of morphospace analysis to macroecological problems would be a valuable step. Such an interaction would be even more interesting with the addition of a stronger functional compo-

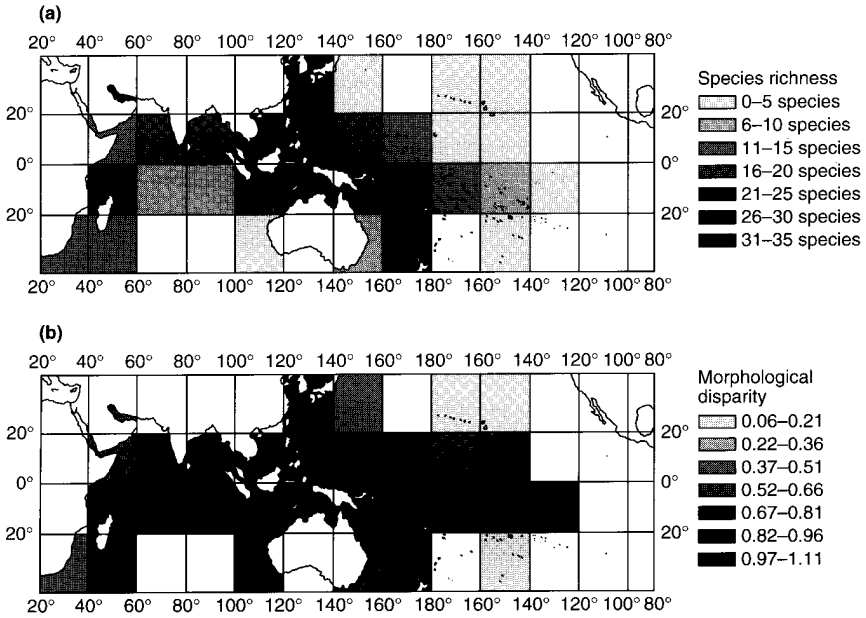


Figure 19.7 Taxonomic (a) and morphological (b) diversity in strombid gastropods of the Indo-West Pacific. Morphological diversity is measured here as disparity, i.e. the geometric mean of the variance of scores on the first six axes of a principal component analysis. (From Roy *et al.* 2001a.)

ment to the palaeo-morphospace work, yielding a synthesis of ecomorphology (e.g. Ricklefs & Miles 1994; Hulsey & Wainwright 2002) and macroecology on evolutionary timescales.

Just as morphological and taxonomic diversity can be decoupled over time, they can be decoupled spatially in the living biota. For example, Roy *et al.* (2001a) showed that spatial patterns of morphological diversity cannot be predicted from data on species richness alone in a large clade of Indo-Pacific gastropods, the Strombidae; regions with relatively few species can still harbour an impressive array of morphologies (Fig. 19.7). The total volume of morphospace occupation correlates fairly well, although non-linearly, with species richness (Fig. 19.8a), but is much more poorly correlated with the dispersion of species within that morphospace (Fig. 19.8b). These plots show that at low species richness the species can be close together or far apart in morphospace, but at high species richness both the total morphospace volume occupied by the clade *and* the spacing among species increases.

Spatial patterns of functional diversity in living molluscs along the northeastern Pacific shelf are also decoupled from taxonomic trends. Species richness of marine bivalves declines by a factor of four from the tropics to the Arctic but the ratio of infaunal species (burrowers such as cockles and razor shells) to epifaunal species

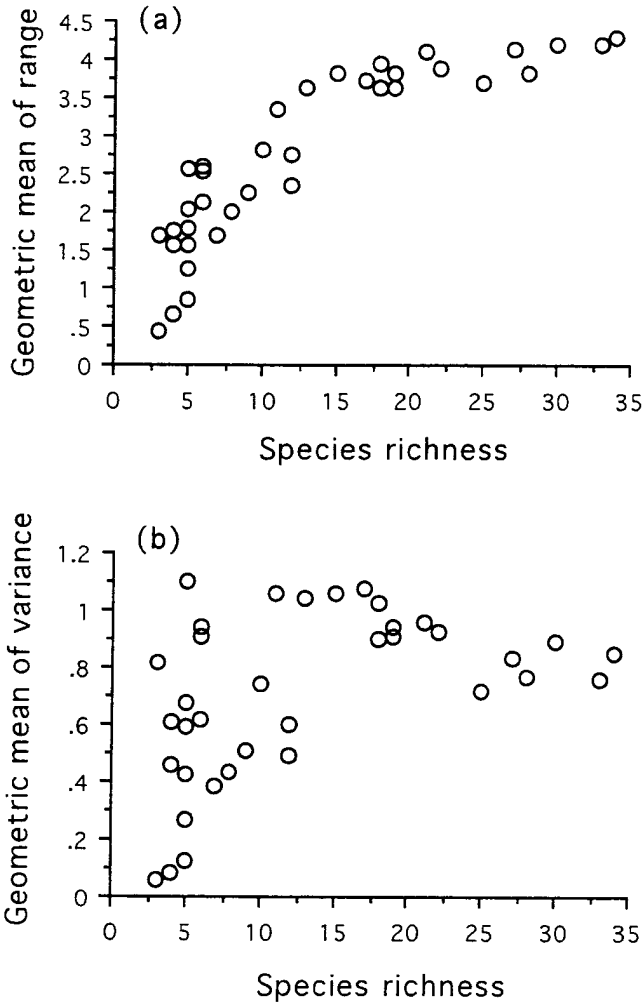


Figure 19.8 Two plots of morphological versus taxonomic diversity in strombids. (a) Morphological diversity as the geometric mean of the *range* of scores on the first six principal components, i.e. the volume of morphospace occupation. (b) Morphological diversity as the geometric mean of the *variance* of scores on the first six axes of a principal component analysis, i.e. the dispersion of morphospace occupation, or disparity. (From Roy *et al.* 2001a.)

(surface-dwellers such as scallops and mussels) increases with latitude (Roy *et al.* 2000b). This contrasts strikingly with the negative slope of the infaunal/epifaunal ratio seen in latest Jurassic bivalves (Tithonian Stage, about 145–150 Ma) (Crame 1996, 2002). Spatial trends in functional diversity can clearly change and even reverse over time, although the underlying processes remain poorly known.

In marine gastropods, trends in functional diversity also tend to be decoupled from trends in species richness (Valentine *et al.* 2002). The steep latitudinal gradient in species richness (Roy *et al.* 1998) contrasts with the non-linear trend in the ratio of carnivorous to non-carnivorous species (Fig. 19.9a). As in bivalves, the processes underlying these trends in gastropod functional diversity remain poorly understood but macroecological processes may play an important role. For example, the fine-scale change in the ratio of gastropod feeding groups is not seen in the ratio at the level of provinces (Fig. 19.9b), indicating more rapid spatial turnover of non-carnivorous species in the temperate zone relative to carnivores there, or relative to either group in the tropics (a given degree of temperate latitude includes fewer overlapping geographical ranges for non-carnivores than carnivores, driving the ratio down on a per-degree basis but keeping it high at the province scale). This, of course, raises the question of whether these differences in distributional patterns largely reflect historical contingencies such as differential extinctions and/or range shifts during Neogene time (Todd *et al.* 2002) or whether they are maintained by ecological processes. Nor do we know much about how the major macroecological variables mentioned above vary among functional groups or how they relate to morphological traits. Palaeontological data have the potential to provide the most direct understanding of the dynamics underlying such large-scale spatial patterns.

A Pleistocene baseline?

Human impacts are increasingly altering every ecosystem on the planet. These changes have produced the shifting baseline syndrome (Pauly 1995; Jackson 1997; Dayton *et al.* 1998), where the ecosystems studied by each generation of ecologists are more degraded than those seen by the previous generation. This syndrome is widespread both on land and in the oceans, from deep-water fisheries to intertidal communities (Jackson 2001; Jackson *et al.* 2001).

Given the magnitude of this environmental disturbance, the Pleistocene and Holocene fossil record may often be our best source for quantifying the relationships among the variables mentioned at the beginning of this chapter. Clearly, the taxonomic richness and abundance structure of many present-day communities are very different from those of just a millennium, a few centuries, or even a few decades ago. This is perhaps most clear for oceanic islands, where the fossil record shows that Polynesians, Melanesians and other 'first arrivals' had a major impact on vertebrate species richness and body-size–frequency distributions (e.g. Steadman 1995; Burney *et al.* 2001; Gaston & Blackburn, this volume). Gaston & Blackburn (2000; p. 297) outline some aspects of macroecology that may be robust to human disruption, such as body-size–life-history trade-offs and other broad features of the biology of species and their interactions with the physical environment. But accurately detecting even these may be problematic in marine ecosystems. For example, intraspecific size distributions of species are being drastically altered by size-selective human predation on marine fish (Jackson *et al.* 2001) and intertidal invertebrates (Pombo & Escofet 1996; Griffiths & Branch 1997; Lindberg *et al.* 1998). These changes are oc-

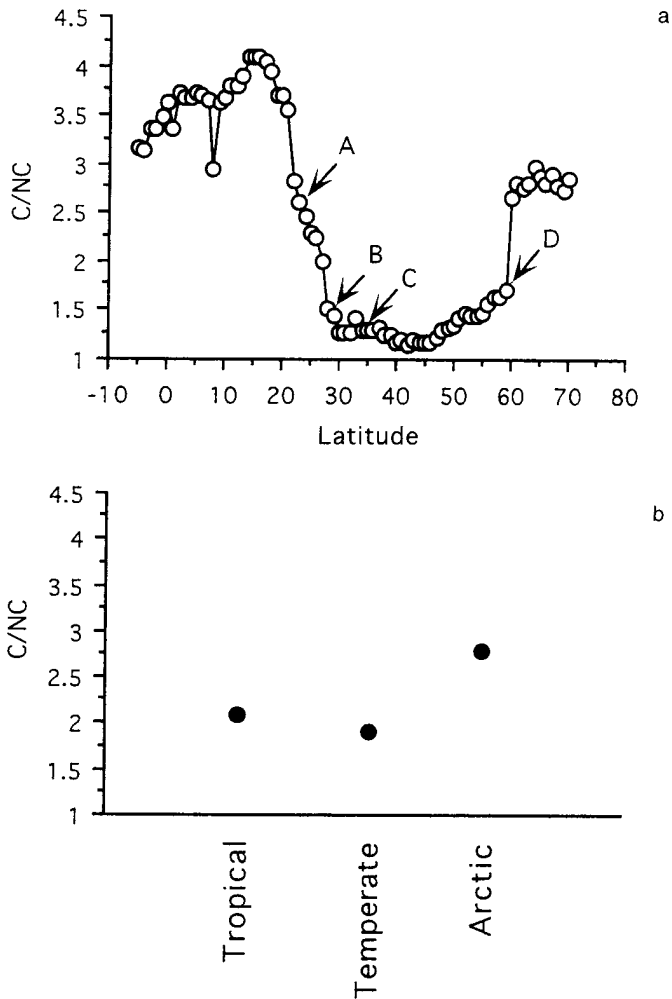


Figure 19.9 Ratio of carnivorous (C) to non-carnivorous (NC) shelled marine gastropods along the eastern Pacific shelf. (a) Plotted for 1° bins; arrows indicate boundaries between molluscan provinces as follows: A, Panamic–Surian; B, Surian–Californian; C, Californian–Oregonian; D, Oregonian–Arctic (after Valentine *et al.* 2002). (b) Same data plotted for major climate zones.

curring in concert with changes in species abundances (Jackson *et al.* 2001). The most effective tests of macroecological hypotheses have been quantitative and not qualitative (e.g. Gaston & Blackburn 1999, 2000; Lawton 1999), hence changes in abundance, body size and maturation age over the past century owing to pressure by fisheries (e.g. Law 2000; Reynolds, this volume) represent distortions in the values of

macroecologically important variables that may obscure fundamental relationships, both among biological variables and between biological and physical parameters. These effects are almost certainly present among terrestrial vertebrates as well, but historical trends are yet to be quantified. Finally, if as the data suggest the most severe perturbations are non-randomly distributed along key environmental gradients (e.g. latitude, altitude and bathymetry), then the stability of latitudinal and other gradients in environmental factors such as temperature mean and variance does not guarantee undistorted correlations to biotic patterns. For many taxa the late Pleistocene and Holocene fossil record provides a pre-human baseline and a fuller picture of the envelope of natural variation in the focal variables than can be gleaned from short-term observations on the present-day biota. Incorporation of such historical data would go a long way towards avoiding the pitfalls of doing macroecology in a world dominated by 'unnatural' ecosystems (*sensu* Jackson 2001).

The fidelity with which fossil assemblages reflect the living associations from which they are recruited is being studied, and the results indicate that it is greater than has been generally realized. Macroecologically important parameters are captured by fossils right across the ecological hierarchy. For example, in the Pleistocene of the northeastern Pacific, the species composition of the entire living molluscan fauna is well-represented (e.g. Valentine 1989), and the bioprovincial framework and community-level associations are preserved (Valentine 1961). Although fossil faunas are time-averaged (i.e. represent the accumulation of individuals over many generations), specific morphological parameters, including measures of allometric ratios and of the variability found in living populations, are commonly preserved (Bush *et al.* 2002). Even more encouraging, Kidwell's (2001) meta-analysis of species abundance data shows that dead shells capture the abundance structure of the corresponding live community. Indeed, the fossil assemblages probably constitute a better sample of regional to local biotas, with their large complement of rare species, than do short-term censuses of live individuals. Thus there are aspects of time-averaging that actually enhance macroecological interpretations.

Conclusion

Not only does a stronger partnership between palaeontology and macroecology have great potential, it is likely to be essential for answering many important questions. Macroecology has largely been dominated by the detection and interpretation of correlations among variables. A deeper understanding of causality requires the analysis of dynamics (as advocated, for example, by Gaston 1998). For many groups, palaeobiological evidence provides the most direct way of quantifying dynamics, by providing data on origination, extinction and other features such as shifts in geographical ranges and morphological diversity, to produce an evolutionary macroecology. The fossil record will help to choose between plausible alternatives, as in the relationship between geographical range and speciation rate (Fig. 19.6). The record is sure to offer surprises as well, such as uncovering the greater volatility of geo-

graphical range in large-bodied bivalves (Figs 19.1–19.3), the indifference of clade evolutionary trajectories to modal body sizes (Fig. 19.4), and the discordance between taxonomic and morphological diversity in time and space (Figs 19.7 and 19.8). On the other hand, modern neontological research draws upon the full range of organisms within the biosphere, and can provide the indispensable knowledge of the physiological and genetic underpinnings of the macroecological parameters, which is the only hope for achieving a fundamental understanding of fossil patterns. The fields of palaeobiology and macroecology are clearly destined to be conjoined.

Summary

For decades, palaeontologists have been studying macroecological aspects of the fossil record, from explicitly dynamic and hierarchical perspectives. The integration of macroecological and macroevolutionary fields into what might be called evolutionary macroecology will be valuable, because dynamics underlying present-day macroecological patterns tend to operate on palaeontological timescales through such processes as speciation, extinction and range shifts. We present examples where the fossil record yields insight into these processes, including the relationship between range shifts and body size, the dynamics of body-size evolution relative to modal values, extinction and geographical range, speciation and geographical range, and the non-linear relationships between functional or morphological diversity and species richness.

Building stronger ties between palaeobiology and neontology will require a serious effort to explore the macroecology of the modern marine biota. It is not clear that marine patterns correspond to those observed on land for the main macroecological variables such as body size, geographical range and abundance; terrestrial and marine processes may be sufficiently distinct that qualitatively different patterns emerge from similar analyses.

The fossil record also demonstrates that species richness and species associations in many regions — islands and mainlands alike — have changed significantly over the past 10 000 years, and even more dramatically over long timescales, owing to extinctions and migrations. This raises serious doubts about the stability of patterns observed on neontological timescales. Palaeontological data thus offer an important baseline for relationships among body size, geographical range, species richness, abundance and other macroecologically important variables subject to alteration by human activities.

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References

- Alroy, J. (1998) Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* **280**, 731–734.
- Blackburn, T.M. & Gaston, K.J. (2001) Linking patterns in macroecology. *Journal of Animal Ecology* **70**, 338–352.
- Bohonak, A.J. (1999) Dispersal, gene flow, and population structure. *Quarterly Review of Biology* **74**, 21–45.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.
- Brown, J.H., Marquet, P.A. & Taper, M.L. (1993) Evolution of body size: consequences of an energetic definition of fitness. *American Naturalist* **142**, 573–584.
- Budd, A.F. & Coates, A.G. (1992) Nonprogressive evolution in a clade of Cretaceous *Montastraea*-like corals. *Paleobiology* **18**, 425–446.
- Budd, A.F. & Johnson, K.G. (2001) Contrasting patterns in rare and abundant species during evolutionary turnover. In: *Evolutionary Patterns* (eds J.B.C. Jackson, S. Lidgard & F.K. McKinney), pp. 295–325. University of Chicago Press, Chicago, IL.
- Burney, D.A., James, H.F., Burney, L.P., *et al.* (2001) Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecological Monographs* **71**, 615–641.
- Bush, A.M., Powell, M.G., Arnold, W.S., Bert, T.M. & Daley, G.M. (2002) Time-averaging, evolution, and morphologic variation. *Paleobiology* **28**, 9–25.
- Chapman, M.G. (1999) Are there adequate data to assess how well theories of rarity apply to marine invertebrates? *Biodiversity and Conservation* **8**, 1295–1318.
- Chown, S.L. (1997) Speciation and rarity: separating cause from consequence. In: *The Biology of Rarity* (eds W.E. Kunin & K.J. Gaston), pp. 91–109. Chapman and Hall, London.
- Ciampaglio, C.N., Kemp, M. & McShea, D.W. (2001) Detecting changes in morphospace occupation patterns in the fossil record: characterization and analysis of measures of disparity. *Paleobiology* **27**, 695–715.
- Clarke, A. (1993) Temperature and extinction in the sea: a physiologist's view. *Paleobiology* **19**, 499–518.
- Cohen, J.E. (1994) Marine and continental food webs: three paradoxes. *Philosophical Transactions of the Royal Society, London, Series B* **343**, 57–69.
- Collin, R. (2001) The effects of mode of development on phylogeography and population structure of North American *Crepidula* (Gastropoda: Calyptraeidae). *Molecular Ecology* **10**, 2249–2262.
- Crame, J.A. (1996) Antarctica and the evolution of taxonomic diversity gradients in the marine realm. *Terra Antarctica* **3**, 121–134.
- Crame, J.A. (2002) Evolution of taxonomic diversity gradients in the marine realm: a comparison of Late Jurassic and Recent bivalve faunas. *Paleobiology* **28**, 184–207.
- Dayton, P.K., Tegner, M.J., Edwards, P.B. & Riser, K.L. (1998) Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications* **8**, 309–322.
- Duncan, R.P., Bomford, M., Forsyth, D.M. & Conibear, L. (2001) High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. *Journal of Animal Ecology* **70**, 621–632.
- Endler, J.A. (1977) *Geographic Variation, Speciation, and Clines*. Princeton University Press, Princeton, NJ.
- Erwin, D.H. (2001) Lessons from the past: biotic recoveries from mass extinctions. *Proceedings of the National Academy of Sciences, USA* **98**, 5399–5403.
- Foote, M. (1996) Models of morphological diversification. In: *Evolutionary Paleobiology* (eds D. Jablonski, D.H. Erwin & J.H. Lipps), pp. 62–86. University of Chicago Press, Chicago, IL.
- Foote, M. (1997) The evolution of morphological diversity. *Annual Review of Ecology and Systematics* **28**, 129–152.
- Foote, M. (1999) Morphological diversity in the evolutionary radiation of Paleozoic and post-Paleozoic crinoids. *Paleobiology Memoir* **1** (Supplement to *Paleobiology* **25**(2)).
- Forys, E.A. & Allen, C.R. (1999) Biological invasions and deletions: community change in south Florida. *Biological Conservation* **87**, 341–347.
- Gaston, K.J. (1998) Species–range size distributions: products of speciation, extinction and

- transformation. *Philosophical Transactions of the Royal Society, London, Series B* **353**, 219–230.
- Gaston, K.J. & Blackburn, T.M. (1999) A critique for macroecology. *Oikos* **84**, 353–368.
- Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and Process in Macroecology*. Blackwell Science, Oxford.
- Gaston, K.J. & Chown, S.L. (1999) Geographic range size and speciation. In: *Evolution of Biological Diversity* (eds A.E. Magurran & R.M. May), pp. 237–259. Oxford University Press, Oxford.
- Gili, C. & Martinell, J. (1994) Relationship between species longevity and larval ecology in nassariid gastropods. *Lethaia* **27**, 291–299.
- Griffiths, C.L. & Branch, G.M. (1997) The exploitation of coastal invertebrates and seaweeds in South Africa: historical trends, ecological impacts and implications for management. *Transactions of the Royal Society of South Africa* **52**, 121–148.
- Hansen, T.A. (1978) Larval dispersal and species longevity in Lower Tertiary gastropods. *Science* **199**, 885–887.
- Hansen, T.A. (1982) Modes of larval development in early Tertiary neogastropods. *Paleobiology* **8**, 367–372.
- Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Hellberg, M.E., Balch, D.P. & Roy, K. (2001) Climate-driven range expansion and morphological evolution in a marine gastropod. *Science* **292**, 1707–1710.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Hulsey, C.D. & Wainwright, P.C. (2002) Projecting mechanics into morphospace: disparity in the feeding system of labrid fishes. *Proceedings of the Royal Society, London, Series B* **269**, 317–326.
- Jablonski, D. (1986a) Larval ecology and macroevolution of marine invertebrates. *Bulletin of Marine Science* **39**, 565–587.
- Jablonski, D. (1986b) Background and mass extinctions: the alternation of macroevolutionary regimes. *Science* **231**, 129–133.
- Jablonski, D. (1987) Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* **238**, 360–363.
- Jablonski, D. (1988) Estimates of species durations. *Science* **240**, 969.
- Jablonski, D. (1993) The tropics as a source of evolutionary novelty: the post-Palaeozoic fossil record of marine invertebrates. *Nature* **364**, 142–144.
- Jablonski, D. (1995) Extinction in the fossil record. In: *Extinction Rates* (eds R.M. May & J.H. Lawton), pp. 25–44. Oxford University Press, Oxford.
- Jablonski, D. (1996) Body size and macroevolution. In: *Evolutionary Paleobiology* (eds D. Jablonski, D.H. Erwin & J.H. Lipps), pp. 256–289. University of Chicago Press, Chicago.
- Jablonski, D. (1997) Body-size evolution in Cretaceous mollusks and the status of Cope's rule. *Nature* **385**, 250–252.
- Jablonski, D. (1998) Geographic variation in the molluscan recovery from the end-Cretaceous extinction. *Science* **279**, 1327–1330.
- Jablonski, D. (2000) Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology. *Paleobiology* **26** (Supplement to Number 4), 15–52.
- Jablonski, D. (2001) Lessons from the past: evolutionary impacts of mass extinctions. *Proceedings of the National Academy of Sciences, USA* **98**, 5393–5398.
- Jablonski, D. (2002) Survival without recovery after mass extinctions. *Proceedings of the National Academy of Sciences, USA* **99**, 8139–8144.
- Jablonski, D. & Lutz, R.A. (1983) Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* **58**, 21–89.
- Jablonski, D. & Raup, D.M. (1995) Selectivity of end-Cretaceous marine bivalve extinctions. *Science* **268**, 389–391.
- Jablonski, D. & Roy, K. (2003) Geographic range and speciation in fossil and living mollusks. *Proceedings of the Royal Society, London, Series B* **270**, 401–406.
- Jablonski, D. & Sepkoski, J.J., Jr. (1996) Paleobiology, community ecology, and scales of ecological pattern. *Ecology* **77**, 1367–1378.
- Jablonski, D. & Valentine, J.W. (1990) From regional to total geographic ranges: testing relationship in Recent bivalves. *Paleobiology* **16**, 126–142.
- Jackson, J.B.C. (1974) Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary consequences. *American Naturalist* **108**, 541–560.
- Jackson, J.B.C. (1997) Reefs since Columbus. *Coral Reefs* **16**, S23–S32.
- Jackson, J.B.C. (2001) What was natural in the

- coastal oceans? *Proceedings of the National Academy of Sciences, USA* **98**, 5411–5418.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., et al. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–638.
- Kammer, T.W., Baumiller, T.K. & Ausich, W.I. (1998) Evolutionary significance of differential species longevity in Osagean–Meramecian (Mississippian) crinoid clades. *Paleobiology* **24**, 155–176.
- Kidwell, S.M. (2001) Preservation of species abundance in marine death assemblages. *Science* **294**, 1091–1094.
- Kittiwattananong, K. (1999) The relation of reproductive modes to population differentiation in marine bivalves and gastropods. *Phuket Marine Biological Center Special Publication* **19**, 129–138.
- Knoll, A.H. & Carroll, S.B. (1999) Early animal evolution: emerging views from comparative biology and evolution. *Science* **284**, 2129–2137.
- Law, R. (2000) Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* **57**, 659–668.
- Lawton, J.H. (1999) Are there general laws in ecology? *Oikos* **84**, 177–192.
- Lindberg, D.R., Estes, J.A. & Warheit, K.I. (1998) Human influences on trophic cascades along rocky shores. *Ecological Applications* **8**, 880–890.
- Lupia, R. (1999) Discordant morphological disparity and taxonomic diversity during the Cretaceous angiosperm radiation: North American pollen record. *Paleobiology* **25**, 1–28.
- Marshall, C.R. (1991) Estimation of taxonomic ranges from the fossil record. In: *Analytical Paleobiology. Short Courses in Paleontology 4* (eds N.L. Gilinsky & P.W. Signor), pp. 19–38. Paleontological Society, Knoxville, TN.
- Maurer, B.A. (1999) *Untangling Ecological Complexity*. University of Chicago Press, Chicago, IL.
- Maurer, B.A. & Nott, M.P. (1998) Geographic range fragmentation and the evolution of biological diversity. In: *Biodiversity Dynamics* (eds M.L. McKinney & J.A. Drake), pp. 31–50. Columbia University Press, New York.
- Maurer, B.A., Brown, J.H. & Rusler, R.D. (1992) The micro and macro in body size evolution. *Evolution* **46**, 939–953.
- Mayr, E. (1963) *Animal Species and Evolution*. Harvard University Press, Cambridge, MA.
- McGhee, G.R. (1999) *Theoretical Morphology*. Columbia University Press, New York.
- McKinney, M.L. (1997a) Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* **28**, 495–516.
- McKinney, M.L. (1997b) How do rare species avoid extinction? A paleontological view. In: *The Biology of Rarity* (eds W.E. Kunin & K.J. Gaston), pp. 110–129. Chapman and Hall, London.
- Miller, A.I. (1998) Biotic transitions in global marine diversity. *Science* **281**, 1157–1160.
- Niklas, K.J. (1997) *The Evolutionary Biology of Plants*. University of Chicago Press, Chicago, IL.
- Pauly, D. (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* **10**, 430.
- Pechenik, J.A. (1999) On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series* **177**, 269–297.
- Pombo, O.A. & Escofet, A. (1996) Effect of exploitation on the limpet *Lottia gigantea*: a field study in Baja California (Mexico) and California (U.S.A.). *Pacific Science* **50**, 393–403.
- Raup, D.M. (1979) Biases in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History* **13**, 85–91.
- Raup, D.M. (1985) Mathematical models of cladogenesis. *Paleobiology* **11**, 42–52.
- Ricklefs, R.E. & Miles, D.B. (1994) Ecological and evolutionary inferences from morphology: an ecological perspective. In: *Ecological Morphology* (eds P.C. Wainwright & S.M. Reilly), pp. 13–41. University of Chicago Press, Chicago, IL.
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Roughgarden, J., Pennington, T. & Alexander, S. (1994) Dynamics of the rocky intertidal zone with remarks on generalization in ecology. *Philosophical Transactions of the Royal Society, London, Series B* **343**, 79–85.
- Roy, K. (1994) Effects of the Mesozoic Marine Revolution on the taxonomic, morphologic and biogeographic evolution of a group: Aporrhaid gastropods during the Mesozoic. *Paleobiology* **20**, 274–296.

- Roy, K. & Foote, M. (1997) Morphological approaches to measuring biodiversity. *Trends in Ecology and Evolution* **12**, 277–281.
- Roy, K. & Martien, K.K. (2001) Latitudinal distribution of body size in north-eastern Pacific marine bivalves. *Journal of Biogeography* **28**, 485–493.
- Roy, K., Jablonski, D., Valentine, J.W., & Rosenberg, G. (1998) Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences, USA* **95**, 3699–3702.
- Roy, K., Jablonski, D. & Martien, K.K. (2000a) Invariant size–frequency distributions along a latitudinal gradient in marine bivalves. *Proceedings of the National Academy of Sciences, USA* **97**, 13150–13155.
- Roy, K., Jablonski, D. & Valentine, J.W. (2000b) Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proceedings of the Royal Society, London, Series B* **267**, 293–299.
- Roy, K., Balch, D.P. & Hellberg, M.E. (2001a) Spatial patterns of morphological diversity across the Indo-Pacific: analyses using strombid gastropods. *Proceedings of the Royal Society, London, Series B* **268**, 2503–2508.
- Roy, K., Jablonski, D. & Valentine, J.W. (2001b) Climate change, species range limits and body size in marine bivalves. *Ecology Letters* **4**, 366–370.
- Roy, K., Jablonski, D. & Valentine, J.W. (2002) Body size and invasion success in marine bivalves. *Ecology Letters* **5**, 163–167.
- Russell, M.P. & Lindberg, D.R. (1988) Real and random patterns associated with molluscan spatial and temporal distributions. *Paleobiology* **14**, 322–330.
- Scheltema, R.S. (1989) Planktonic and non-planktonic development among prosobranch gastropods and its relationship to the geographic range of species. In: *Reproduction, Genetics and Distribution of Marine Organisms* (eds J.S. Ryland & P.A. Tyler), pp. 183–188. Olsen & Olsen, Fredensborg, Denmark.
- Scheltema, R.S. (1992) Passive dispersal of planktonic larvae and the biogeography of tropical sublittoral invertebrate species. In: *Marine Eutrophication and Population Dynamics* (eds G. Colombo *et al.*), pp. 195–202. Olsen and Olsen, Fredensborg, Denmark.
- Sepkoski, J.J., Jr. (1991) A model of onshore–off-shore change in faunal diversity. *Paleobiology* **17**, 58–77.
- Smith, A.B. (1994) *Systematics and the Fossil Record*. Blackwell Science, Oxford.
- Stanley, S.M. (1979) *Macroevolution*. W.H. Freeman, San Francisco.
- Stanley, S.M. (1990) The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages. In: *Causes of Evolution* (eds R.M. Ross & W.D. Allmon), pp. 103–127. University of Chicago Press, Chicago, IL.
- Steadman, D.W. (1995) Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science* **267**, 1123–1131.
- Steele, J.H., Carpenter, S.R., Cohen, J.E., Dayton, P.K. & Ricklefs, R.E. (1993) Comparing terrestrial and marine ecological systems. In: *Patch Dynamics* (eds S.A. Levin, T.M. Powell & J.H. Steele), pp. 1–12. Springer-Verlag, Berlin, New York.
- Strathmann, R.R. (1990) Why life histories evolve differently in the sea. *American Zoologist* **30**, 197–207.
- Thomas, R.D.K., Shearman, R.M. & Stewart, G.W. (2000) Evolutionary exploitation of design options by the first animals with hard skeletons. *Science* **288**, 1239–1242.
- Todd, J.A., Jackson, J.B.C., Johnson, K.G., *et al.* (2002) The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene. *Proceedings of the Royal Society, London, Series B* **269**, 571–577.
- Valentine, J.W. (1961) Paleocologic molluscan geography of the Californian Pleistocene. *University of California Publications in Geological Sciences* **34**, 309–442.
- Valentine, J.W. (1973) *Evolutionary Paleocology of the Marine Biosphere*. Prentice-Hall, Englewood Cliffs, NJ.
- Valentine, J.W. (1989) How good was the fossil record? Clues from the Californian Pleistocene. *Paleobiology* **15**, 83–94.
- Valentine, J.W. (1995) Why no new phyla after the Cambrian? Genome and ecospace hypotheses revisited. *Palaio* **10**, 190–194.
- Valentine, J.W., Foin, T.C. & Peart, D. (1978) Provincial model of Phanerozoic diversity. *Paleobiology* **4**, 55–66.
- Valentine, J.W., Jablonski, D. & Erwin, D.H. (1999) Fossils, molecules and embryos: new perspectives

- on the Cambrian explosion. *Development* **126**, 851–859.
- Valentine, J.W., Roy, K. & Jablonski, D. (2002) Carnivore/noncarnivore ratios in northeastern Pacific marine gastropods. *Marine Ecology Progress Series* **228**, 153–163.
- Veltman, C.J., Nee, S. & Crawley, M.J. (1996) Correlates of introduction success in exotic New Zealand birds. *American Naturalist* **147**, 542–557.
- Vermeij, G.J. (1994) The evolutionary interaction among species: selection, escalation, and coevolution. *Annual Review of Ecology and Systematics* **25**, 219–236.
- Wagner, P.J. & Erwin, D.H. (1995) Phylogenetic patterns as tests of speciation models. In: *New Approaches to Speciation in the Fossil Record* (eds D.H. Erwin & R.L. Anstey), pp. 87–122. Columbia University Press, New York.
- Wills, M.A., Briggs, D.E.G. & Fortey, R.A. (1994) Disparity as an evolutionary index: a comparison of Cambrian and Recent arthropods. *Paleobiology* **20**, 93–130.