

CHAPTER 5

Lessons from the fossil record: the Ediacaran radiation, the Cambrian radiation, and the end-Permian mass extinction

Stephen Q. Dornbos, Matthew E. Clapham, Margaret L. Fraiser, and Marc Laflamme

5.1 Introduction

Ecologists studying modern communities and ecosystems are well aware of the relationship between biodiversity and aspects of ecosystem functioning such as productivity (e.g. Tilman 1982; Rosenzweig and Abramsky 1993; Mittelbach *et al.* 2001; Chase and Leibold 2002; Worm *et al.* 2002), but the predominant directionality of that relationship, whether biodiversity is a consequence of productivity or vice versa, is a matter of debate (Aarssen 1997; Tilman *et al.* 1997; Worm and Duffy 2003; van Ruijven and Berendse 2005). Increased species richness could result in increased productivity through 1) interspecies facilitation and complementary resource use, 2) sampling effects such as a greater chance of including a highly productive species in a diverse assemblage, or 3) a combination of biological and stochastic factors (Tilman *et al.* 1997; Loreau *et al.* 2001; van Ruijven and Berendse 2005).

The importance of burrowing organisms as ecosystem engineers that influence ecosystem processes in the near-seafloor environment has gained increasing recognition (e.g. Thayer 1979; Seilacher and Pflüger 1994; Marinelli and Williams 2003; Solan *et al.* 2004; Mermillod-Blondin *et al.* 2005; Ieno *et al.* 2006; Norling *et al.* 2007; Solan *et al.* 2008). Increased bioturbation influences the benthic ecosystem by increasing the water content of the uppermost sediment layers, creating a diffuse mixed layer

and altering substrate consistency (Thayer 1979; Seilacher and Pflüger 1994). In addition, burrowing organisms play a crucial role in modifying decomposition and enhancing nutrient cycling (Solan *et al.* 2008).

Increased species richness often enhances ecosystem functioning, but a simple increase in diversity may not be the actual underlying driving mechanism; instead an increase in functional diversity, the number of ecological roles present in a community, may be the proximal cause of enhanced functioning (Tilman *et al.* 1997; Naeem 2002; Petchey and Gaston, 2002). The relationship between species richness (diversity) and functional diversity has important implications for ecosystem functioning during times of diversity loss, such as mass extinctions, because species with overlapping ecological roles can provide functional redundancy to maintain productivity (or other aspects of functioning) as species become extinct (Solan *et al.* 2004; Petchey and Gaston, 2005).

5.2 Strengths and limitations of the geological record

The fossil record provides an unparalleled, nearly 600 million year-long history of changing diversity in marine animal ecosystems. This extensive deep-time history provides a series of natural experiments in changing biodiversity, ranging from rapid

diversification during the radiation of metazoans in the Ediacaran and the Cambrian explosion to extensive species losses during mass extinctions such as the Permian-Triassic crisis. The fossil record is also the only source of potential analogues to challenges facing the biosphere in the near future. Situations such as ice-free climates, rapid greenhouse gas emission and global warming, or the extinction of nearly 80% of marine invertebrate genera are not available for study on the modern Earth, yet are all represented in the fossil record.

Despite incomplete preservation, most notably of species that lack hard parts like shells or bone, the fossil record retains a recognizable signal of changes in biodiversity. Measures of diversity are particularly reliable in exceptionally preserved localities (Lagerstätten) containing soft tissue preservation, such as the Cambrian Burgess Shale or Chengjiang Fauna (Allison and Briggs 1993; Dornbos *et al.* 2005) or the latest Precambrian Ediacara biota (Clapham *et al.* 2003; Droser *et al.* 2006), but localities with typical hard part-only preservation can still provide useful data, although with more caveats (Kidwell, 2002; Tomašových and Kidwell, 2010). The loss of soft tissues, along with preservation biases against certain types of shell mineralogy (Cherns and Wright 2009), precludes comparison of shelly fossil collections with extant communities but does not prevent comparison among different fossil assemblages. The typical shelly fossil assemblage contains a mixture of individuals that originally lived over a span of decades to millennia ('time averaging'), not preserved in life position but mostly derived from within a particular habitat ('spatial mixing'). Time averaging inflates species richness relative to any single life assemblage (Kidwell 2002), a problem that becomes increasingly pronounced with increasing temporal scales of time averaging (Tomašových and Kidwell 2010). These effects introduce random noise to the biodiversity signal, reducing the precision of potential analyses and conclusions. Biodiversity changes can nevertheless be resolved and other ecological attributes, such as the relative-abundance structure of the shell-bearing taxa within a community, are preserved with greater fidelity (Kidwell 2002).

Proxies for ecosystem functioning may be more difficult to obtain, however, and there are several factors that complicate reconstruction of the productivity-diversity relationship in nearly all fossil assemblages. Most experimental analyses of the productivity-diversity relationship are conducted in assemblages of primary producers (terrestrial plant assemblages); thus, productivity can be measured directly as biomass or the rate of biomass accumulation (e.g. Tilman *et al.* 1997; Worm and Duffy 2003). We will use this definition of productivity throughout the chapter. In contrast, the marine fossil record, at least in the Phanerozoic (the time of conspicuous animals, since the Cambrian Explosion), is dominated by heterotrophic, primarily suspension- and deposit-feeding, invertebrates. Because they are not primary producers, their diversity is unlikely to have direct effects on primary production as postulated for plant assemblages (Tilman *et al.* 1997; Worm and Duffy 2003; van Ruijven and Berendse 2005). The combined biomass of heterotrophic invertebrates is presumably influenced to some degree by food supply, however, suggesting that biotic or stochastic factors (e.g. facilitation, niche complementarity, sampling effects; Tilman *et al.* 1997; Loreau *et al.* 2001) could similarly influence the biomass-diversity relationship.

Although food supply is influenced by primary productivity, it is difficult to relate primary productivity to nutrient levels, which are more commonly inferred through geological proxies, because of the complicated controls on primary production (Braisner 1995). Even nutrient levels themselves are difficult to assess in the ancient record. First, quantitative geochemical proxies for paleoproductivity, such as accumulation rates of the mineral barite (Dymond *et al.* 1992; Paytan and Griffith 2007) or trace metal (Cd, Cu, Ni, Zn) concentrations (Piper and Perkins 2004; Piper and Calvert 2009), rely on accurate age models of sedimentation rates that are typically only available in deep-sea sediment cores or other fine-grained mudrocks (Paytan and Griffith 2007). However, nearly all sedimentary deposition on the continental shelf, the depositional environment for almost all invertebrate fossil localities, is episodic and punctuated by numerous hiatuses of unknown but typically geologically short duration.

Second, total organic carbon (TOC) concentrations reflect a complex signal of not only primary productivity but also dilution by accumulating inorganic sediment particles such as clay minerals, preservation versus degradation in surface sediments (Calvert *et al.* 1992; Lee 1992; Ganeshram *et al.* 1999), and subsequent alteration during deep burial (e.g. Pell *et al.* 1993). Although quantitative geochemical proxies are not available, time-averaged estimates of productivity can be obtained from calculations of biomass (e.g. Clapham *et al.* 2003) or trends in shell abundance or body size of marine invertebrates (e.g. Fraiser and Bottjer 2004). Shell abundance is affected by the same factors that complicate geochemical proxies (sediment dilution, shell destruction), and body size may reflect other influences, such as greater juvenile mortality or shortened lifespans due to harsh environmental conditions. Nevertheless, the density and/or size of fossil taxa provide a reasonable proxy for biomass, which itself is related to productivity (Waide *et al.* 1999).

Evidence for burrowing activity in marine sediments, or bioturbation, is readily observable in the fossil record through preserved trace fossils (also called ichnofossils). Although the uppermost levels of the mixed layer are rarely preserved, except when marine substrates were firmly consolidated (Droser *et al.* 2002), maximum burrow depth and burrow diameters can readily be measured from preserved trace fossils (Droser and Bottjer 1988; Droser *et al.* 2002; Marenco and Bottjer 2011). The intensity of sediment mixing can be measured independently using the semi-quantitative ichnofabric index method, which scores sedimentary beds on a scale of 1–5 depending on the amount of disruption to original depositional features (Droser and Bottjer 1986). An ichnofabric index of 1 corresponds to absent—or extremely minimal—bioturbation, such that original layering and features are preserved, whereas ichnofabric index 5 corresponds to complete homogenization of the layer. Thus, ichnofabric index measures and quantification of burrow size and depth provide a good proxy for sediment mixing rates and the ecosystem functions—such as nutrient recycling—associated with bioturbation.

Functional diversity is difficult to quantify even in modern settings (Petchev *et al.* 2004), and it is unlikely that the biological requirements and ecological contributions of extinct taxa can be known with similar precision. Paleontologists have a long history, however, of grouping extinct taxa into broader functional guilds using attributes such as life position—e.g. benthic versus planktonic, epifaunal versus infaunal—motility, and trophic mode (e.g. Bambach, 1983; Bambach *et al.* 2007; Bush and Bambach 2011; Bush *et al.* 2011). These characteristics can be reliably determined for the vast majority of fossil taxa, even for extinct groups such as trilobites (Fortey and Owens 1999), and provide a coarse proxy for functional diversity. Additional aspects of functional diversity have been described in terms of tiering—sometimes called stratification in the biological literature—the vertical subdivision of epifaunal or infaunal habitat space, presumably indicative of niche partitioning (—e.g. Ausich and Bottjer 1982; Clapham and Narbonne 2002).

In this chapter, we explore three of these critical biodiversity changes: 1) the Ediacaran radiation of large multicellular eukaryotes, 2) the Cambrian radiation of complex bilaterian-grade animals, and 3) the end-Permian mass extinction, the largest known extinction event in Earth history. For each of these events, we examine how changes in biodiversity were related to various factors involved in ecosystem functioning such as productivity, bioturbation (biogenic mixing depth), and functional diversity.

5.3 Ediacaran ecosystems

For the first three billion years of its existence, life on Earth was dominated by microorganisms. The appearance in the latest Ediacaran (578–542 Mya) of large, soft-bodied, and structurally complex multicellular eukaryotes colloquially called the Ediacara biota marked a fundamental change in the way ecosystems are built and sustained (Narbonne 2005; Xiao and Laflamme 2009). Despite sharing a similar age and mode of preservation, most Ediacara biota represent an assemblage of unrelated organisms. Some Ediacaran fossils represent the oldest animals and perhaps root stock to modern faunas (Fedonkin

and Waggoner 1999), while others represent extinct clades lying outside of crown Metazoa (Narbonne 2004; Xiao and Laflamme 2009). Despite this taxonomic uncertainty, temporal, biogeographic, and species-diversity patterns in Ediacaran localities highlight the existence of three assemblages characterized by distinct evolutionary innovations (Waggoner 2003):

1) The Avalon assemblage of Mistaken Point in Newfoundland and Bradgate Park in England (578–560 Mya) is an entirely deep-water assemblage, having formed several hundred meters below storm wave base and the photic zone (Wood *et al.* 2003; Wilby *et al.* 2011). As a result, the Ediacara biota from these localities could not utilize sunlight as their primary source of energy. The Avalon assemblage is dominated by rangeomorphs, an extinct clade of organisms constructed almost entirely from repeatedly branched (fractal) units and temporally restricted to the Ediacaran (Figure 5.1; Narbonne 2004; Narbonne *et al.* 2009; Brasier and Antcliffe 2009). This fractal branching allowed the rangeomorphs to attain high surface-area to volume ratios necessary for diffusion-based feeding, termed osmotrophy (Sperling *et al.* 2007; Laflamme *et al.* 2009). In the absence of metazoan zooplankton and macropredators in the Ediacaran, and as a result a lack of sloppy feeding and egestion, a greater portion of labile dissolved organic carbon was able to reach the deep ocean to be consumed by osmotrophes (Sperling *et al.* 2011). Trace-fossils from the Avalon assemblage are rare and restricted to the surface (Liu *et al.* 2010), while carbonate skeletons are unknown.

2) The White Sea assemblage (560–550 Mya), best known from the Flinders Ranges in South Australia and the White Sea coast of Russia, marks a significant step in metazoan evolution, with the first appearance of likely bilaterians (Fedonkin and Waggoner 1997; Fedonkin 2007) and a diverse array of novel trace fossils. The highest diversity of fossils from the White Sea assemblage occurs in rocks that were deposited in well-lit and energetically active shallow water (Gehling 2000). The White Sea assemblage postdates a major change in the stable carbon isotope composition (ratio of ^{13}C to ^{12}C) of lime-

stones that has been (contentiously) interpreted as an oxidation of a large deep ocean dissolved organic carbon pool (Rothman *et al.* 2003; Fike *et al.* 2006).

3) The Nama assemblage (550–541 Mya) of Namibia marks a further step in the progression towards modern ecosystems with the advent of biologically mediated secretion of calcium carbonate skeletons (Figure 5.1; Grotzinger *et al.* 1995).

The underlying cause for the segregation of the Ediacara biota into three assemblages is difficult to isolate (Waggoner 2003; Grazhdankin 2004; Narbonne 2005) and could have been influenced, at least in part, by important differences in the way fossils were preserved in each locality (Narbonne 2005). Biological responses to limiting factors associated with changes in bathymetry could also explain the diversity pattern, as the Avalon assemblage represents a deep-water community, while the most diverse and fossiliferous White Sea and Nama assemblages occupied significantly shallower water settings. Most intriguingly, however, the increased diversity and ecological complexity could instead reflect evolutionary advances from the oldest Avalon assemblage, through the younger White Sea assemblage containing the first mobile bilaterians, to the youngest Nama assemblage with its biomineralizing taxa (Xiao and Laflamme 2009; Brasier *et al.* 2010a).

The unusual style of fossil preservation in Ediacaran communities allows potential relationships between diversity and ecosystem functioning, including productivity, bioturbation, and functional diversity, to be examined more rigorously. In contrast to virtually all other fossil assemblages, which are time-averaged and have undergone some degree of spatial mixing, most Ediacaran assemblages record a snapshot of the original *in situ* community of soft-bodied organisms as it appeared at the moment of death (Seilacher 1992; Gehling 1999; Clapham *et al.* 2003). Any dead specimens (Liu *et al.* 2010) would decay within days to weeks (Allison 1988; Brasier *et al.* 2010b; Darroch *et al.* submitted), orders of magnitude smaller than typical time averaging in shelly communities (several hundred years; Kowalewski *et al.* 1998), and on the same timeframe as modern ecological census population studies.

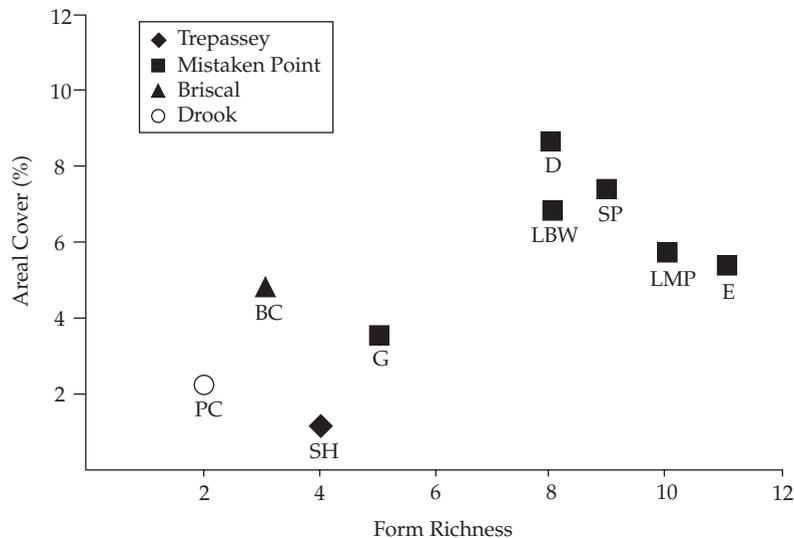


Figure 5.1 Richness-areal coverage relationship for Ediacaran communities from the Avalon Assemblage, Newfoundland. Genus richness is approximated by form richness, although informal groups such as ‘dusters’ may actually include several genera. The probable microbial structures *Ivesheadia* and the informally named ‘lobate discs’ are excluded. Areal coverage is a proxy for three-dimensional biomass and is measured as the percentage of the rock outcrop covered by fossil impressions, also excluding the area accounted for by *Ivesheadia* and ‘lobate discs.’ Although areal coverage in the most diverse surfaces is lower than the peak value, maximum likelihood estimation strongly supports a linear model fit (Akaike weight 0.91, compared to 0.055 for Gaussian and 0.035 for quadratic fits).

This nearly unique style of preservation allows investigation of ecological questions that may be obscured in the younger fossil record. For example, did more productive Ediacaran communities have higher species richness? What effects did the onset of bioturbation have on diversity in younger Ediacaran communities? Was there positive feedback between increasing functional diversity and higher species richness, in the form of facilitation or niche partitioning (Laflamme and Narbonne 2008b)?

5.3.1 Productivity–biodiversity relationship

Using organic carbon (TOC) as a proxy for productivity in Ediacara biota assemblages is not possible because of complications from dilution by sediment input and degradation during burial of the sedimentary strata, as discussed above. In addition, TOC levels in fossiliferous Ediacaran units are uniformly low: < 0.2 weight % in Newfoundland (Canfield *et al.* 2007), < 0.2 wt % in South Australia

(Calver 2000), and < 0.1 wt % in Namibia (Kaufman *et al.* 1991). Although paleoproductivity cannot be quantified in any Ediacaran fossil assemblage, the unusual preservation of the autotrophic (likely osmotrophic) fossils as ‘snapshots’ of the living community does allow estimation of standing biomass, analogous to ecological approaches (e.g. Tilman *et al.* 1997), and its relationship to diversity (Clapham and Narbonne, 2002; Clapham *et al.* 2003; Droser *et al.* 2006; Wilby *et al.* 2011). As productivity is the rate of biomass creation, biomass measures provide an approximation of time-averaged productivity over the lifespan of the organisms (Waide *et al.* 1999), although biomass and productivity at any given instant may themselves be interrelated (Guo 2007). Because the three-dimensional shape and material properties are unknown for most Ediacaran fossils, biomass can only be approximated by calculating the percentage of the rock surface covered by fossils—percent areal cover (Clapham *et al.* 2003). Areal cover is compared with ‘form diversity,’ an approximation of species

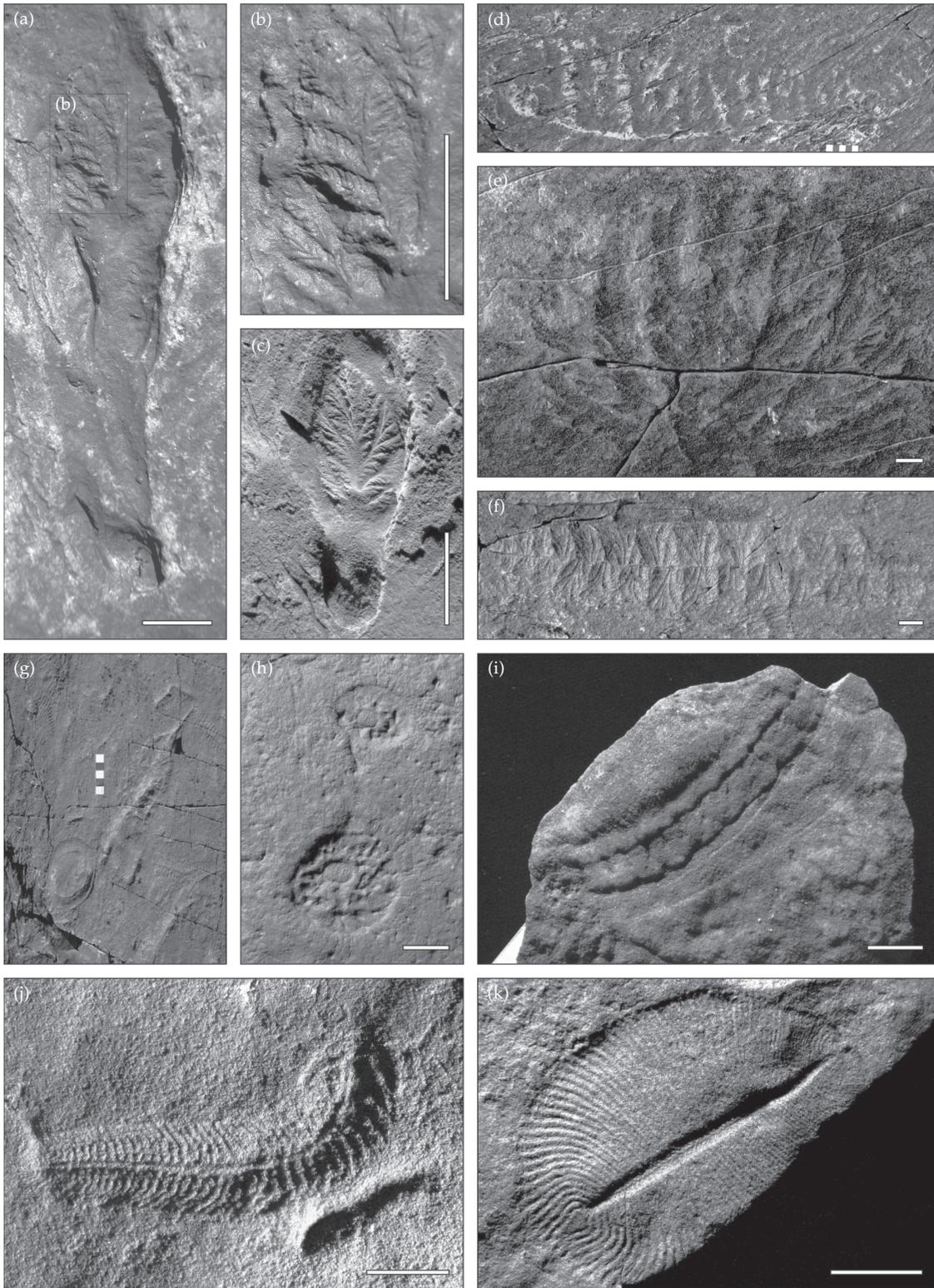
diversity that takes the presence of undescribed taxa—such as ‘dusters’, which may represent several genera (Clapham *et al.* 2003)—into account. Taxa such as *Ivesheadia* and the undescribed ‘lobate disc’ were included in the areal coverage calculations in Clapham *et al.* (2003) but are excluded here—except for Long Beach West (LBW) and Spaniard’s Bay (SP) surfaces as taxon-specific areal coverage data are not available for those localities—because those taxa likely represent microbial mat structures rather than multicellular eukaryotes (Laflamme *et al.* in press; although see Liu *et al.* 2010). The exclusion of ivesheadiomorphs from the analysis also eliminates some of the time-averaging issues raised by Lui *et al.* 2011.

Sample size is small and the data are noisy, but there is a weakly significant positive relationship ($r = 0.68$, $p = 0.04$) between form richness—‘diversity’—and areal cover—‘biomass’—in Avalon assemblages at Mistaken Point (Figure 5.1). Although there is a significant linear correlation, peak areal coverage does not occur at maximum form richness (Figure 5.1), potentially suggestive of a unimodal—‘hump-shaped’—relationship commonly, but not always, observed in modern communities (e.g. Waide *et al.* 1999; Worm and Duffy 2003; van Ruijven and Berendse 2005; Guo 2007). Maximum likelihood estimation was used to fit and compare linear, Gaussian, and quadratic models to discriminate between linear and unimodal-richness areal cover relationships at Mistaken Point. The linear model receives the substantial proportion of model support (Akaike weight 0.91), whereas Gaussian (Akaike weight 0.055) and quadratic (Akaike weight 0.035) models are poor fits to the data. However, Ediacaran communities span a limited range of richness values—less than 10 form taxa per site—and could potentially occupy one limb of a larger unimodal trend. Ongoing paleoecological research in the Flinders Ranges, South Australia (White Sea Assemblage; Droser *et al.* 2006) may also help extend and clarify trends interpreted from Avalonian assemblage communities at Mistaken Point. Nevertheless, the correlation based on existing data tentatively suggests that richer Ediacaran communities had greater biomass,

therefore also were more productive, although the existence or directionality of causation (whether productivity led to greater diversity or vice versa) cannot be determined.

5.3.2 Influence of bioturbation on ecosystem functioning

The Ediacaran interval marks the onset of animal bioturbation and its ecological effects: infaunal bioturbation is absent in the oldest Ediacaran communities (Avalon assemblage) and simple horizontal traces are first found in the younger White Sea assemblage (Seilacher *et al.* 2005; Jensen *et al.* 2006). The first appearance of trace fossils in the White Sea assemblage corresponds with an increase in ecological complexity and the appearance of a variety of new functional groups, including mobile grazing metazoans, but does not correspond with an increase in within-community richness (Narbonne 2005; Bottjer and Clapham 2006; Droser *et al.* 2006; Shen *et al.* 2008). A causal relationship between the two events is unlikely, however, because Ediacaran bioturbation was extremely sparse and entirely represented by surficial traces that did not rework the sediment (Seilacher *et al.* 2005; Jensen *et al.* 2006). It is more likely that the appearance of new functional groups, including mobile animals, reflects some combination of permissive environmental conditions—such as an increase in oxygen levels—ecological feedbacks, or simply continuing biological evolution. Frondose taxa, which had been highly dominant in the oldest Avalon assemblage (Laflamme *et al.* 2004; 2007; Narbonne *et al.* 2009) and were highly adapted to firm microbial substrates (Seilacher 1999; Laflamme *et al.* 2010), were also less important constituents of the White Sea assemblage (Bottjer and Clapham 2006; Droser *et al.* 2006). Frondose taxa and mobile grazers appear to have been largely segregated in White Sea assemblage communities (Droser *et al.* 2006), suggesting that the decline of erect frondose forms may have resulted from sediment disturbance by mobile mat-grazers and/or burrowers. However, bioturbation did not have a significant vertical component that would lead to appreciable sediment reworking until



the Cambrian (Droser and Bottjer 1988; Droser *et al.* 2002), at which point it did exert an important control on marine ecosystems (Bottjer *et al.* 2000).

5.3.3 Species richness–functional diversity relationship

Ediacaran communities display a trend of increasing species richness from the earliest Avalonian examples to the White Sea assemblage, accompanied by a corresponding trend towards greater functional diversity. Ediacaran functional diversity cannot be quantified due to the uncertain life habits of many of the taxa (Xiao and Laflamme 2009), but it is possible to make some qualitative generalizations regarding changes in the types of functional groups represented. Early Avalon assemblage communities, in the Drook and Briscal Formations, had low species richness (3–5 form species present) and also had low functional diversity and poorly developed epifaunal stratification (referred to as tiering in the paleontological literature). The two dominant taxa in the Pigeon Cove community—*Charnia* and *Thectardis*—were both relatively unspecialized erect mid-to-upper-tier feeders (Clapham and Narbonne, 2002; Laflamme *et al.* 2007; Sperling *et al.* 2011). The third, *Ivesheadia*, is unlikely to be a metazoan (Liu *et al.* 2010; Laflamme *et al.* in press). The younger Bristy Cove community was nearly exclusively populated by low-tier rangeomorphs (e.g. *Fractofusus*, *Beothukis*) that fed from the basal few centimeters of the water column. In contrast, richness and functional diversity were both higher in later Avalonian communities, especially in the Mistaken Point Formation. Although those communities were still dominated by rangeomorphs, taxa began to display morphological adaptations for subdividing ecospace such as a differentiation of

their body into a separate food-gathering apparatus and elevating stem (Laflamme *et al.* 2004; Laflamme and Narbonne 2008a, 2008b). Well-developed epifaunal tiering also resulted in a much more precise subdivision of the vertical habitat: the D surface community at Mistaken Point contained *Fractofusus* in the lowest tier, *Bradgatia* at an intermediate level, *Pectinifrons* at greater heights, and *Beothukis* in the upper level at heights of nearly 30 cm (Figure 5.2; Clapham and Narbonne 2002; Laflamme and Narbonne, 2008b). Comparison of the ecological structure of low- and high-diversity Avalon communities indicates that high-diversity communities had a broader range of organism heights subdivided into a more complex and regular tiering structure. Thus, the positive relationship between species richness and functional diversity was plausibly driven by niche partitioning and development of a more finely subdivided tiering structure in Avalon assemblage communities.

In the White Sea assemblage, fronds still dominated the upper tiers while the lowermost tiers were colonized by attached epibenthic recliners such as *Tribrachidium*, *Arkarua*, *Parvoancorina* (Figure 5.2), and *Phyllozoon* (Droser *et al.* 2006). Mobile *Kimberella* (Figure 5.2; Fedonkin and Waggoner 1997; Fedonkin 2007; Ivantsov 2009) and *Dickinsonia* (Figure 5.2; Gehling *et al.* 2005; Sperling and Vinther 2010), both of which grazed on abundant microbial mats, also make their appearance in the White Sea assemblage; as the first mobile, non-suspension feeding (or absorbing) taxa, they indicate a major increase in functional diversity. However, this increase in functional diversity—perhaps the most significant ecological change within the Ediacaran—was not accompanied by an increase in within-community species richness, or morphospace expansion (Shen *et al.* 2008), although the regional species pool was

Figure 5.2 Diversity of Ediacaran organisms. (a–f) represent various members of the rangeomorpha from Newfoundland. (a) *Avalofractus abaculus* from the Trepassy Fm. at Spaniard's Bay, with long stem and close-up (b) of a fractal, rangeomorph frondlet. (c) *Beothukis mistakensis* (NFM F-758) from the Trepassy Fm. at Spaniard's Bay. (d) Fence-shaped *Pectinifrons abyssalis* from the Mistaken Point Fm. at Mistaken Point North. (e) Cabbage-shaped *Bradgatia linfordensis* (ROM36500) from the Mistaken Point Fm. 'd' surface at Mistaken Point. (f) Spindle-shaped *Fractofusus misrai* from the Mistaken Point Fm. 'e' surface at Mistaken Point. (g) Frondose *Charniodiscus spinosus* from the Mistaken Point Fm. 'e' surface at Mistaken Point. (h–k) Assortment of classic Ediacaran organisms from the Flinders Ranges in South Australia. (h) Two specimens of the probable sponge *Palaeophragmodictya reticulata* (P32352a–f). (i) Probable stem-group mollusk *Kimberella quadrata* (P23532). (j) Bilaterally-symmetrical *Spriggina floundersi* (P12771) with anterior-posterior differentiation. (k) Probable placozoan *Dickinsonia costata* (P18888). Scale bars 1 cm or 1 cm increments.

substantially larger in the White Sea assemblage. Richness and evenness values in White Sea communities from Australia—mean richness of 5.25 species per bedding plane—are not significantly different from those in Avalon communities from Newfoundland (Droser *et al.* 2006).

Increased functional richness in younger White Sea assemblage Ediacaran communities, even though assemblage-level species richness was similar to the older Avalon assemblage, implies that Australian communities had lower functional redundancy. Australian assemblages also had more variable species composition and relative abundances (Droser *et al.* 2006), whereas Mistaken Point communities contain many of the same species, albeit at different abundances, over more than 10 million years of their history (Clapham *et al.* 2003). Community stability in the Avalon assemblage may reflect the stabilizing role of functional redundancy, allowing maintenance of community structure during disturbances (Naeem 1998). However, it is difficult to definitively reconstruct the true relationship between stability and functional redundancy because of the overprint of environmental parameters such as the frequency of disturbance. The significantly different habitats of the two assemblages—deep marine continental slope for the Avalon assemblage, coastal shallow marine for the White Sea assemblage—may instead be primarily responsible for increased volatility in community composition in the Australian examples.

5.4 Cambrian ecosystems

Ecosystems continued to increase in complexity during the Cambrian radiation (starting at 542 Mya). This event involved the geologically rapid diversification of marine animal life into relatives of nearly all modern phyla. This increase in diversity was coupled with increasing ecological complexity as active animals began interacting with each other on a large scale. Although their precursors might lie in the Ediacaran, it is in the Cambrian that we find the first definitive evidence for predation, the first widespread biomineralization, the first macroscopic sensory organs, and the first development of the seafloor mixed layer through bioturbation (Bottjer

et al. 2000; Bengtson 2002, 2004; Plotnick *et al.* 2010; Callow and Brasier 2009). It was indeed a time of rapid restructuring of marine ecosystems.

Lagerstätten deposits, which provide the highest definition view of animal life during the Cambrian radiation due to their preservation of soft tissues, are particularly abundant during the early and middle Cambrian, and then fade into comparative rarity through the remainder of the Phanerozoic Eon (Allison and Briggs 1993). Two of the most well studied Lagerstätten assemblages are the early Cambrian Chengjiang biota of Yunnan Province, China, and the middle Cambrian Burgess Shale biota of British Columbia, Canada. Priapulid worms and arthropods are dominant in the Chengjiang biota, and arthropods dominate the Burgess Shale biota (Dornbos *et al.* 2005; Caron and Jackson 2008; Zhao *et al.* 2009).

5.4.1 Productivity–biodiversity relationship

The rapid early Cambrian diversification and radiation of phytoplankton fossils provides evidence for a dramatic increase in primary productivity during the Cambrian radiation (e.g. Butterfield 1997). These fossils consist of small acanthomorphic acritarchs, thought to be fossil remnants of planktonic eukaryotic algae (Butterfield 1997). These fossils are accompanied by the first evidence for mesozooplankton, consisting of minute feeding structures preserved alongside the acritarchs (Butterfield 1997).

The development of multiple trophic levels in the planktonic realm was an important characteristic of the Cambrian radiation (Butterfield 1997), and most likely would have facilitated the further revolution of suspension-feeding benthic organisms, as consolidated organic particles became more common in marine waters. It is also likely that the evolution of zooplankton led to the restriction of a large percentage of primary productivity, and as such labile dissolved organic carbon (DOC), to the surface ocean where it is rapidly consumed and recycled through the microbial loop (Azam *et al.* 1983; Pomeroy *et al.* 2007). Furthermore, the evolution of fecal pellets clumped organic waste into ballasted packages that could travel through the water column to accumulate as detritus on the seafloor

(Logan *et al.* 1995). As such, the deep oceans likely became impoverished in labile DOC, which would have had a dramatic effect on deep ocean osmotrophic Ediacarans which relied on DOC and could not capture and process larger particulates favored by filter-feeding cnidarians and sponges (Sperling *et al.* 2011). The increasing complexity that developed near the base of the marine trophic web during the Cambrian radiation clearly played a role in the dramatic increase in biodiversity that is one of the signatures of this critical event in the evolutionary history of animals (Butterfield 2009).

5.4.2 Influence of bioturbation on ecosystem functioning

Trace fossil taxa diversified rapidly during the Cambrian radiation, reflecting the increasing complexity of animal behavior (e.g. McLroy and Logan 1999; Droser *et al.* 2002). Bioturbation depth and intensity increased accordingly within a broad spectrum of Cambrian depositional environments (Droser 1987). Evidence for a well-developed mixed layer in the upper few centimeters of the seafloor is found for the first time in the Cambrian, and paleoecological studies of benthic suspension feeders indicates that it had a profound effect on ecosystem functioning (Seilacher 1999; Bottjer *et al.* 2000; Dornbos 2006).

Echinoderms are among the earliest skeletonized sessile benthic suspension feeders in the Phanerozoic, and have therefore been the focus of many studies aimed at understanding the evolutionary response of benthic organisms to mixed layer development during the Cambrian. Early and middle Cambrian echinoderms include many genera adapted to living directly attached to, or inserted in, firm unlithified sediments (Bottjer *et al.* 2000; Dornbos 2006). By the late Cambrian, however, all sessile benthic echinoderms lived attached to hard substrates, either rare carbonate hardgrounds or loose shell material. This trend away from direct interaction with unlithified sediments and toward hard substrate attachment through the Cambrian is consistent with an evolutionary response to the development of the mixed layer in marine sediments.

Examination of the substrate adaptations of sessile benthic suspension feeders in the early Cambrian Chengjiang biota supports the pattern seen in early echinoderms. From the perspective of both generic diversity and relative abundance, forms adapted to firm unlithified sediments dominate the Chengjiang biota (Dornbos *et al.* 2005; Dornbos and Chen 2008). This would be expected given the early Cambrian age of the fossil assemblage, as mixed layer development was only beginning. Direct examination of the sediments in which these fossils are preserved indeed reveals that bioturbation levels were minimal (Dornbos *et al.* 2005). Similar data from the Burgess Shale biota is limited, but suggests that fewer sessile suspension-feeding genera were adapted for direct substrate interaction (Dornbos *et al.* 2005).

The increasing bioturbation depth and intensity through the Cambrian clearly was one critical factor in shaping ecosystem functioning. Sessile benthic taxa were placed under strong selective pressure to adapt to increased sediment mixing, resulting in the evolution of new attachment structures and strategies.

5.4.3 Species richness–functional diversity relationship

There was a remarkable increase in animal species richness from the Ediacaran into the Cambrian. This increase in richness was also associated with a marked increase in functional diversity, as measured by ecospace occupation (e.g. Bambach *et al.* 2007). When comparing ecospace occupation during the Ediacaran and Cambrian Periods, it becomes clear that a major shift took place from relatively large, mostly immobile animals in the Ediacaran, to somewhat smaller but more mobile animals in the Cambrian (Bambach *et al.* 2007; Xiao and Laflamme 2009). Most of the immobile Ediacaran animals were most likely absorbing dissolved organic carbon from the seawater, while the smaller immobile Cambrian animals are interpreted as suspension feeders on organic particles. Mobile Cambrian animals occupied a wide range of ecospace compared their mobile Ediacaran counterparts (Bambach *et al.* 2007), which were also much more rare.

Indeed, it is during the Cambrian in which we find the first definitive evidence for macrophagous predation, widespread skeletonization, macroscopic sensory organs, and intense bioturbation of the seafloor (Bottjer *et al.* 2000; Bengtson 2002, 2004; Plotnick *et al.* 2010). Evidence for these ecological changes is found throughout the early and middle Cambrian fossil record, but is even more apparent in deposits of exceptional preservation, such as the Chengjiang and Burgess Shale biotas. The older Chengjiang biota is particularly informative because of its early Cambrian age, which places it during the heart of Cambrian radiation. In this assemblage, we find the oldest evidence for the largest known Cambrian predators, the well-known stem group arthropods known as the anomalocaridids (e.g. Whittington and Briggs 1985). Well-developed eyes and mechano- and chemosensory organs are also found preserved in many Chengjiang taxa, indicating the importance of navigating the Cambrian marine landscape in search of prey, mates, or protection from predators (Plotnick *et al.* 2010).

5.5 The end-Permian mass extinction and its aftermath

The Great Ordovician Biodiversification Event (GOBE) 485–460 Mya exhibited a greater increase in biodiversity at the family, genus, and species levels than the Cambrian Explosion, and was associated with increases in tiering, epifaunal modes of life, and bioturbation (Servais *et al.* 2010). The GOBE established the Paleozoic Evolutionary Fauna that was dominant approximately 488–251 Mya (Ogg *et al.* 2008), and characterized as having intermediate-diversity communities, common epifaunal suspension feeders, developing tiering, and intermediate complexity food webs (Sheehan 1996). The end of the Paleozoic era and the dominance of the Paleozoic Evolutionary Fauna were marked by the end-Permian mass extinction ~252 Mya. This extinction was the largest mass extinction since the Cambrian radiation, whereby 78% of marine genera, and 49% and 63% of marine and terrestrial families disappeared (Raup and Sepkoski 1982; Clapham *et al.* 2009).

5.5.1 Environmental changes during the late Paleozoic to early Mesozoic

By the Late Carboniferous to Early Permian, Earth's major continents were configured as the supercontinent Pangea (Scotese 1997). Atmospheric carbon dioxide levels were low during the Permo-Carboniferous, while atmospheric oxygen levels were at their zenith in the Early Permian (Berner 2004). The precise cause of the end-Permian mass extinction remains controversial, but it is generally well-accepted that the ultimate cause of the extinction was massive volcanism leading to a cascade of environmental effects (Riccardi *et al.* 2007). Some combination of hypercapnia (carbon dioxide toxicity), hydrogen sulfide toxicity, and climate change, triggered or catalyzed by the eruption of the Siberian Traps, appears to be the most likely kill mechanism (Kump *et al.* 2005; Knoll *et al.* 2007). Deep-water anoxic and euxinic conditions developed in the Middle (Isozaki 1997) and Late Permian (Nielsen and Shen 2004), indicating that environmental stress that led to the Paleozoic-Mesozoic biotic crisis was likely to have been initiated several million years before the end-Permian mass extinction. Geochemical and sedimentological data also indicate that anoxia, euxinia, and high CO₂ concentrations in the oceans persisted at least intermittently through the Early Triassic (Pruss *et al.* 2006; Takahashi *et al.* 2009).

5.5.2 Permian–Triassic marine nutrient levels and primary productivity

Modeling supports the hypothesis that global warming during the Permian through Triassic would have decreased the equator to pole temperature gradient, thereby lowering wind velocities, thermohaline circulation, upwelling intensities, transport of nutrients to the deep ocean and to surface waters, and thus primary productivity (Kidder and Worsely 2004). However, some sedimentological and geochemical proxies indicate that nutrient levels and primary productivity may have fluctuated spatially and temporally during the late Permian through Early Triassic.

Hypotheses have been proposed for both enhanced and decreased input of continental

nutrients into the marine realm during the Late Permian to Early Triassic. Modeling suggests that because mountain building had ceased, silicate weathering decreased, and thus nutrient input into the oceans was minimal and led to a crash in primary productivity in the Late Permian (Kidder and Worsley 2004). On the contrary, the extinction of land plants, the occurrence of pedoliths, and a rise in strontium isotopic values through the Early Triassic indicate that terrestrial primary productivity decreased rapidly, soil erosion was drastic, and continental weathering increased (Korte *et al.* 2003; Sephton *et al.* 2005; Sheldon 2006; Hu *et al.* 2008; Huang *et al.* 2008; Sedlacek *et al.* 2008; Ward *et al.* 2005; Retallack *et al.* 2005). The increased transport of terrestrial sediments and nutrients into the marine realm is proposed to have facilitated eutrophication, possibly increasing primary productivity in the ocean (Sephton *et al.* 2005).

The Early Triassic has a unique sedimentological record for the Phanerozoic that can also serve as a proxy for nutrient levels (e.g. Pruss *et al.* 2006). There is little documented organic matter in Lower Triassic strata, despite conditions that would have contributed to organic matter production and preservation—including low oxygen conditions, the phosphate cycle, and low bioturbation (e.g., Berner and Canfield 1989; Wignall and Twitchett 1996). Organic-rich black shales have been found in southwest Japan, Australia, and the Sverdrup basin in northern Canada, and are hypothesized to have resulted from increased nutrients via rivers or upwelling, or enhanced preservation under anoxic conditions (Suzuki *et al.* 1998; Thomas *et al.* 2004; Grasby and Beauchamp 2009). The possibility exists that high TOC was recorded in some Lower Triassic strata that has not yet been discovered (Suzuki *et al.* 1998; Golonka *et al.* 1994; Thomas *et al.* 2004).

Prior to the end-Permian mass extinction, there was a long episode of global chert accumulation termed the Permian Chert Event (PCE) (Isozaki 1994; Beauchamp and Baud 2002). It is proposed that the PCE was facilitated by upwelling of nutrient- and silica-rich water along north-western Pangea as seasonal melting of northern sea ice led to circulation of these waters (Beauchamp and Baud 2002; Kidder and Worsley 2004). The Early Triassic

was a time of very little biogenic chert production and/or preservation around the world, termed the Early Triassic Chert Gap (ETCG) (Racki 1999; Beauchamp and Baud 2002; Kidder and Worsley, 2004; Takemura *et al.* 2003). Sluggish thermohaline circulation caused by global warming, and low bioavailable nutrients that must be present in sufficient amounts for biogenic siliceous sediments to precipitate during the Early Triassic may have caused a breakdown in the conditions favorable for chert production, accumulation, and preservation (Laschet 1984; Racki 1999; Gammon *et al.* 2000). Alternate hypotheses for the ETCG include a decrease in biogenic silica due to the extinction of some sponge groups (Kato *et al.* 2002; Sperling and Ingle 2006) and a poor record of radiolarians (De Wever *et al.* 2006).

Extensive pyrite deposition is another characteristic feature of rocks deposited during the end-Permian mass extinction and post-extinction aftermath (Grasby and Beauchamp 2009). Prominent pyrite deposition suggests euxinic conditions that would have stripped essential bioavailable trace elements from the seawater (Grasby and Beauchamp 2009) that would have stressed marine primary producers (Anbar and Knoll 2002).

Phosphorites are rare during the Early Triassic, possibly indicating decreased nutrient input and upwelling intensity (Trappe 1994; Kidder and Worsley 2004). The distribution of phosphorites in mid-high latitudes suggests that there may have been a shift in ocean productivity to high latitudes because of changes in chemical weathering patterns (and the resultant P-flux to the ocean) due to the hot and arid climate (Trappe 1994) and wind-driven upwelling. Modeling by Hotinski *et al.* (2001) show that nutrients in high latitudes must have been high in order for H₂S and CO₂ to build up in the ocean.

Permian-Triassic sections around the world record several negative and positive excursions in $\delta^{13}\text{C}$ (Corsetti *et al.* 2005 and references therein; Kaiho *et al.* 2005; Galfetti *et al.* 2007; Haas *et al.* 2007; Hays *et al.* 2007; Grasby and Beauchamp; 2009), which reflect, in part, fluctuations in primary productivity (Suzuki *et al.* 1998; Berner 2002; Payne and Kump 2007). A drop in marine primary productivity has been proposed as one major cause of

the negative shifts (e.g. Grard *et al.* 2005; Rampino and Caldeira 2005; Haas *et al.* 2006, 2007). In euxinic settings, trace metals become scarce and lead to severe nitrogen limitation, which could reduce primary productivity (Anbar and Knoll 2002). That euxinia is recorded in strata immediately before the negative shift in C-isotopes strongly suggests that a global euxinic event may have had a significant negative impact on bioavailable nutrients required to support ocean primary productivity during the Late Permian (Grasby and Beauchamp 2009). $\Delta^{34}\text{S}$ and $\Delta^{13}\text{C}$ values are interpreted in some strata to record a crash in primary productivity in the Late Permian perhaps of up to 50% (Algeo *et al.* 2010).

The anoxic conditions that would have facilitated decreasing primary productivity would have also increased it through phosphorus recycling, since phosphorus is a key nutrient driving productivity (Payne and Kump 2007). A productivity bloom during the Permian-Triassic interval would have occurred when autotrophs recovered, creating a positive excursion in the C-isotope record (Grard *et al.* 2005). Thus productivity crashes were likely to have been followed by productivity blooms that could have been major factors in causing the delayed biotic recovery by consuming oxygen in the photic zone and reducing Earth's capability of CO_2 draw-down (Winguth and Maier-Reimer 2005; Suzuki *et al.* 1998; Kidder and Worsely 2004).

Direct evidence of productivity is indicated by fossils of planktonic and benthic producers. Early-Middle Triassic phytoplankton assemblages were characterized by low biodiversity and widespread blooms of opportunistic acritarchs and prasino-phytes that were likely to have formed the base of Early Triassic marine ecosystem (Eshet *et al.* 1995; Krassilov *et al.* 1999; Afonin *et al.* 2001; Grice *et al.* 2005; Payne and van de Schootbrugge 2007). Intermittent euxinic surface water and nitrogen limitation could have facilitated the blooms of cyanobacteria recorded in Lower Triassic strata, as they are able to fix nitrogen (Anbar and Knoll 2002; Xie *et al.* 2005; Grice *et al.* 2005).

Calcareous algae are rare in the benthic realm during the Early Triassic (see Payne and Van de Schootbrugge 2007). However, microbialites (microbially mediated calcareous structures, *sensu*

Riding 2000) and other microbially mediated structures (such as wrinkle structures) are widespread geographically and occur throughout the Early Triassic (Pruss *et al.* 2006; Baud *et al.* 2005). The fabrics and frameworks of most Early Triassic microbialites were most likely to have been built by calcified coccoid and filamentous cyanobacteria (Lehrmann 1999; Thomas *et al.* 2004; Hips and Haas 2006; Jiang *et al.* 2008). The proliferation of benthic primary producers is hypothesized to have been facilitated by decreased bioturbation, and upwelling of supersaturated, nutrient-rich anoxic marine water (e.g. Pruss *et al.* 2006; Kershaw *et al.* 2007).

5.5.3 Productivity–biodiversity–biomass relationship

Approximately 78% of marine invertebrate genera went extinct at the end of the Permian period (Clapham *et al.* 2009). Molluscs, brachiopods, echi- noderms, bryozoans, and Porifera are the only higher taxa with known macroscopic benthic fossil representatives in the Early Triassic (Griffin *et al.* 2010); 143 genera of bivalves, gastropods, and brachiopods have been identified (Fraiser *et al.* 2010). The mean alpha diversity of Early Triassic collections of skeletonized benthic organisms ranges from 3.67 to 4.19 depending on the preservation style of the fossils (Fraiser *et al.* 2010). The diversity of trace fossils, the tracks and trails of organisms, was also low, ranging from 0–11 ichnogenera (Fraiser and Bottjer 2007). The end-Permian extinction has been correlated with a decline in primary productivity. Some nektonic organisms, like cephalopods, diversified quickly after the extinction, and may indicate an increase in diversity and abundance of primary producers (Brayard *et al.* 2009).

Decreases in bioturbation, animal size, and the abundance of fossil grains in thin- sections suggest that a decrease in animal biomass occurred across the Permian-Triassic boundary and persisted nearly to the end of the Early Triassic (e.g. Payne *et al.* 2006; Fraiser and Bottjer 2007). Tallies from bulk samples and analysis of fossil accumulations indicate that bivalves and microgastropods—gastropods with greatest dimension less than 1 cm—comprised the majority of animal biomass

during the Early Triassic (Fraiser and Bottjer 2004, 2007; Fraiser *et al.* 2005). It has been proposed that reduced Early Triassic animal biomass can be attributed to increased global temperatures, small body sizes, and decreased growth efficiency of bacterial heterotrophs that could not sustain large numbers of molluscs with high metabolic demands (Payne and Finnegan 2006). Opportunistic blooms of cyanobacteria did not necessarily facilitate animal diversification or an increase in biomass because they are not as effective of a food source as eukaryotic algae (see references in Payne and Finnegan 2006).

Yet a decline in abundance and quality of primary productivity cannot explain why organisms with low growth efficiency (i.e. molluscs), instead of those with high growth efficiency (i.e. brachiopods), proliferated around the globe during the aftermath of the end-Permian mass extinction. Fraiser and Bottjer (2007) proposed that microgastropods and bivalves were able to survive the chemically and/or physiologically harsh environmental conditions during the Early Triassic better than most skeletonized benthic marine invertebrates because of their distribution in shallow marine environments and their physiological attributes. Thus, though diversity was very low, some taxa were present in very high numbers likely because they were able to cope with the environmental conditions (e.g. Fraiser and Bottjer 2004).

5.5.4 Discussion

Though fluctuations in nutrient levels and primary productivity contributed to the biotic crisis during the Late Permian through Early Triassic, it is more likely that other factors were more important influences on the extinction and its recovery. Environmental conditions, such as euxinia, most likely directly caused extinctions among both microscopic primary producers and macroscopic organisms (Bottjer *et al.* 2008). Conversely, nutrient levels and primary productivity could have been affected by the decline in biodiversity and biomass as well. Low bioturbation levels might have reduced nutrient recycling in the water column (e.g. Thayer 1983).

Some changes in community structure persisted only during the Early Triassic, while other aspects of benthic level-bottom shallow marine communities were permanently altered. A decrease in biodiversity, the numerical dominance of a few taxa, and the proliferation of microbially-mediated structures represent perhaps the most significant short-term changes in ecosystem functioning that lasted up to 5 million years (Pruss *et al.* 2006; Fraiser and Bottjer 2008; Alroy *et al.* 2008). Some short-term changes, such as a decrease in bioturbation and the proliferation of microbial structures, resemble Cambrian ecosystems (Bottjer *et al.* 1996; Fraiser and Bottjer 2007). Examples of lasting changes in ecosystem function related to the end-Permian mass extinction and its aftermath include the switch in taxonomic and ecologic dominants (Fraiser and Bottjer 2007) and a shift to more complex ecosystems (Bambach *et al.* 2002; Wagner *et al.* 2006). Some of the short-term changes may have facilitated the long-term changes: bivalves may have been aided by firm, microbially mediated substrates onto which they could byssally attach (Fraiser and Bottjer 2007). A complex interplay of environmental mechanisms directly and indirectly caused the extinction and delayed biotic recovery.

5.6 Conclusions

The biodiversity changes associated with the Ediacaran radiation, the Cambrian radiation, and the end-Permian mass extinction provide natural deep-time experiments on the impact of such biodiversity shifts on ecosystem functioning, informing our study of the modern biodiversity crisis. The biodiversity increases associated with the Ediacaran and Cambrian radiations show that ecosystem functioning is enhanced by such changes, making ecosystems more complex and stable in a series of positive feedback loops that increase productivity, bioturbation levels, and functional diversity. The opposite is true of the dramatic loss of marine biodiversity associated with the end-Permian mass extinction. Ecosystem instability lasted for up to 5 million years following this extinction event, with large crashes and blooms in productivity, decreased bioturbation of marine sediments, and sharply decreased functional diver-

sity. These patterns validate the modern emphasis on protecting marine biodiversity, as its decline can foster devastating ecosystem instability that can last far beyond human timescales.

References

- Aarssen, L. W. (1997) High productivity in grassland ecosystems: Effected by species diversity or productive species? *Oikos* **80**:183–4.
- Afonin, S. A., Barinova, S. S., and Krassilov, V. A. (2001) A bloom of zygnematalean green algae *Tympanicysta* at the Permian-Triassic boundary. *Geodiversitas* **23**: 481–487.
- Algeo, T. J., Hinnov, L., Moser, J., Maynard, J. B., Elswick, E., Kuwahara, K., and Sano, H. (2010) Changes in productivity and redox conditions in the Panthalassic Ocean during the latest Permian. *Geology* **38**: 187–190.
- Allison, P. A. (1988) The decay and mineralization of proteinaceous macrofossils. *Paleobiology* **14**:139–54.
- Allison, P.A. and Briggs, D.E.G. (1993) Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology* **21**: 605–8.
- Anbar, A.D., and Knoll, A.H. (2002) Proterozoic ocean chemistry and evolution: a bioorganic bridge? *Science* **297**: 1137–1142.
- Ausich, W. I. and Bottjer, D. J. (1982) Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. *Science* **216**:173–4.
- Azam, F., Fenchel, T., Field, J.G. *et al.* (1983) The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* **10**: 257–63.
- Bambach, R. K. (1983) Ecospace utilization and guilds in marine communities through the Phanerozoic. In: *Biotic Interactions in Recent and Fossil Benthic Communities*, Tevesz, M. J. S. and McCall, P. L. (eds), Plenum Press, New York, 719–46.
- Bambach, R. K., Knoll, A. H., and Sepkoski, J. J. Jr. (2002) Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. *Proceedings of the National Academy of Sciences, USA* **99**: 6954–6959.
- Bambach, R. K., Bush, A. M. and Erwin, D. (2007) Autecology and the filling of ecospace: key metazoan radiations. *Palaeontology* **50**:1–22.
- Beauchamp, B., and Baud, A. (2002) Growth and demise of Permian biogenic chert along northwest Pangea: evidence for end-Permian collapse of thermohaline circulation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **187**: 37–63.
- Bengtson, S. (2002) Origins and early evolution of predation. *The Paleontological Society Special Papers* **8**: 289–317.
- Bengtson, S. (2004) Early skeletal fossils. In: Neoproterozoic-Cambrian Biological Revolutions. Lipps, J.H. and Waggoner, B.M. (eds), *The Paleontological Society Special Papers* **10**: 67–77.
- Berner, R. A. and Canfield, D. E. (1989) A new model for atmospheric oxygen over Phanerozoic time. *American Journal of Science* **289**: 333–381.
- Berner, R.A. (2002) Examination of hypotheses for the Permo-Triassic boundary extinction by carbon cycle modeling. *Proceedings of the National Academy of Science USA* **99**: 4172–4177.
- Berner, R.A. (2004) *The Phanerozoic Carbon cycle: CO₂ and O₂*. Oxford University Press, New York.
- Bottjer, D.J., Schubert, J.K., and Droser, M.L. (1996) Comparative evolutionary palaeoecology: assessing the changing ecology of the past. In: Hart, M. B. (Ed.), *Biotic Recovery from Mass Extinction Events*. Geological Society Special Publication **102**: 1–13.
- Bottjer, D. J., Hagadorn, J. W. and Dornbos, S. Q. (2000) The Cambrian substrate revolution. *GSA Today* **10**(9):1–7.
- Bottjer, D. J. and Clapham, M. E. (2006) Evolutionary paleoecology of Ediacaran benthic marine animals. In: Xiao, S. and Kaufman, A. J. (eds), *Neoproterozoic Geobiology and Paleobiology*. Springer, The Netherlands, 91–114.
- Bottjer, D.J., Clapham, M.E., Fraiser, M.L., and Powers, C.M. (2008) Understanding mechanisms for the end-Permian mass extinction and the protracted Early Triassic aftermath/recovery. *GSA Today* **18**: 4–10.
- Braiser, M.D. (1995) Fossil indicators of nutrient levels. 1: Eutrophication and climate change. In: Bosence, D.W.J. and Allison, P.A. (eds), *Marine Palaeoenvironmental Analysis from Fossils*. Geological Society Special Publication, London, **83**: 113–32.
- Brasier, M.D. and Antcliffe, J. B. (2009) Evolutionary relationships within the Avalonian Ediacara biota: new insights from Laser Analysis. *Journal of the Geological Society*, **166**: 363–84.
- Brasier, M.D., Antcliffe, J. B. and Callow, R. H. T. (2010a) Evolutionary trends in remarkable preservation across the Ediacaran-Cambrian transition and the impact of Metazoan Mixing. In: Allison, P. and Bottjer, D.J. (eds), *Taphonomy: Process and Bias Through Time*. Springer, Dordrecht, 519–67.
- Brasier, M.D., Callow, R., Menon, L. *et al.* (2010b) Osmotrophic biofilms: from modern to ancient. In: Seckbach, J. and Oren, A. (eds), *Microbial Mats. Modern and Ancient Microorganisms in Stratified Systems*, Springer, Dordrecht, 131–48.
- Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Bruhwiler, T., Goudemand, N., Galfetti, T., and Guex, J. (2009) Good genes and good luck: Ammonoid diversity

- and the end-Permian mass extinction. *Science* **325**: 1118–1121.
- Bush, A.M. and Bambach, R. K. (2011) Paleoeologic Megatrends in Marine Metazoa. *Annual Review of Earth and Planetary Sciences* **39**:241–69.
- Bush, A.M., Bambach, R. K. and Erwin, D. (2011) Ecospace Utilization During the Ediacaran Radiation and the Cambrian Eco-explosion In: Laflamme, M., Schiffbauer, J.D. and Dornbos, S.Q. (eds), *Quantifying the Evolution of Early Life: Numerical Approaches to the Evaluation of Fossils and Ancient Ecosystems, Topics in Geobiology Series* **36**:111–33, Springer, Dordrecht.
- Butterfield, N.J. (1997) Plankton ecology and the Proetozoic-Phanerozoic transition. *Paleobiology* **23**: 247–62.
- Butterfield, N.J. (2009) Macroevolutionary turnover through the Ediacaran transition: ecological and biogeochemical implications. In: Craig, J., Thurow, J., Thusu, B., Whitham, A., Abutarruma, Y. (eds), *Global Neoproterozoic Petroleum Systems: The Emerging Potential in North Africa*. Geological Society of London, London, 55–66.
- Callow, R.H.T. and Brasier, M. D. (2009) Remarkable preservation of microbial mats in Neoproterozoic siliclastic settings: Implications for Ediacaran taphonomic models: *Earth-Science Reviews* **96**: 207–19.
- Calver, C. R. (2000) Isotope stratigraphy of the Ediacarian (Neoproterozoic III) of the Adelaide Rift Complex, Australia, and the overprint of water column stratification. *Precambrian Research* **100**:121–50.
- Calvert, S. E., Bustin, R. M. and Pedersen, T. F. (1992) Lack of evidence for enhanced preservation of sedimentary organic matter in the oxygen minimum of the Gulf of California. *Geology* **20**:757–60.
- Canfield, D. E., Poulton, S. W. and Narbonne, G. M. (2007) Neoproterozoic deep-ocean oxygenation and the rise of animal life. *Science* **315**:92–5.
- Caron, J.B. and Jackson, D. A. (2008) Paleoeology of the Greater Phyllopod Bed community, Burgess Shale. *Palaeogeography, Palaeoclimatology, Palaeoecology* **258**: 222–56.
- Chase, J. M. and Leibold, M. A. (2002) Spatial scale dictates the productivity-biodiversity relationship. *Nature* **416**:427–30.
- Cherns, L. and Wright, V. P. (2009) Quantifying the impacts of early diagenetic aragonite dissolution on the fossil record. *Palaios* **24**:756–71.
- Clapham, M. E. and Narbonne, G. M. (2002) Ediacaran epifaunal tiering. *Geology*, **30**:627–30.
- Clapham, M. E., Narbonne, G. M. and Gehling, J. G. (2003) Paleoeology of the oldest-known animal communities: Ediacaran assemblages at Mistaken Point, Newfoundland. *Paleobiology* **29**:527–44.
- Clapham, M.E., Shen, S.Z., and Bottjer, D.J. (2009) The double mass extinction revisited: re-assessing the severity, selectivity, and causes of the end-Guadalupian biotic crisis (Late Permian). *Paleobiology* **35**: 33–51.
- Corsetti, F.A., Baud, A., Marengo, P.J., and Richoz, S. (2005) Summary of Early Triassic carbon isotope records. *Comptes Rendus Palevol* **4**: 473–486.
- Daroch, S., Laflamme, M., Schiffbauer, J. D. et al. Submitted. Experimental Formation of a Microbial Death Mask. *Palaios*.
- De Wever, P., O'Dougherty, L., Gorican, S. (2006) The plankton turnover at the Permo-Triassic boundary, emphasis on radiolarians. *Eclogae geologicae Helvetiae* **99**: S49–S62.
- Domke, K.L. and Dornbos, S.Q. (2010) Paleoeology of the middle Cambrian edrioasteroid echinoderm *Totiglobus*: Implications for unusual Cambrian morphologies. *Palaios* **25**: 209–14.
- Dornbos, S.Q. (2006) Evolutionary palaeoecology of early epifaunal echinoderms: Response to increasing bioturbation levels during the Cambrian radiation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **237**: 225–39.
- Dornbos, S.Q. and Bottjer, D.J. (2000) Evolutionary paleoecology of the earliest echinoderms: Helicoplacoids and the Cambrian substrate revolution. *Geology* **28**: 839–42.
- Dornbos, S.Q. and Bottjer, D.J. (2001) Taphonomy and environmental distribution of helicoplacoid echinoderms. *Palaios* **16**: 197–204.
- Dornbos, S.Q., Bottjer, D.J. and Chen, J.Y. (2005) Paleoeology of benthic metazoans in the Early Cambrian Maotianshan Shale biota and Middle Cambrian Burgess Shale biota: Evidence for the Cambrian substrate revolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* **220**: 47–67.
- Dornbos, S.Q. and Chen, J.Y. (2008) Community palaeoecology of the Early Cambrian Maotianshan Shale biota: Ecological dominance of priapulid worms. *Palaeogeography, Palaeoclimatology, Palaeoecology* **258**: 200–12.
- Droser, M. L. and D. J. Bottjer. (1986) A semiquantitative field classification of ichnofabric. *Journal of Sedimentary Research* **56**:558–9.
- Droser, M.L. (1987) *Trends in depth and extent of bioturbation in Great Basin Precambrian-Ordovician strata, California, Nevada, and Utah*. Ph.D. Dissertation, University of Southern California, 365 p.
- Droser, M. L. and D. J. Bottjer. (1988) Trends in depth and extent of bioturbation in Cambrian carbonate marine environments, western United States. *Geology* **16**:233–6.

- Droser, M. L., Gehling, J. G. and Jensen, S. R. (2006) Assemblage palaeoecology of the Ediacara biota: the unabridged edition? *Palaeogeography, Palaeoclimatology, Palaeoecology* **232**:131–47.
- Droser, M. L., Jensen, S. and Gehling, J. G. (2002) Trace fossils and substrates of the terminal Proterozoic-Cambrian transition: implications for the record of early bilaterians and sediment mixing. *Proceedings of the National Academy of Sciences, USA* **99**:12572–6.
- Dymond, J., Suess, E. and Lyle, M. (1992) Barium in deep-sea sediment: a geochemical proxy for paleoproductivity. *Paleoceanography* **7**:163–81.
- Eshet, Y., Rampino, M.R., Visscher, H. (1995) Fungal event and palynological record of ecological crisis and recovery across the Permian-Triassic boundary. *Geology* **23**: 967–970.
- Fedonkin, M. A. (2007) New data on *Kimberella*, the Vendian mollusc-like organism (White Sea region, Russia): palaeoecological and evolutionary implications. In: Vickers-Rich, P. and Komarow, P. (eds), *The Rise and Fall of the Ediacaran Biota*. Geological Society, London, Special Publications 2007; v. 286; 157–79.
- Fedonkin, M. A. and Waggoner, B. M. (1997) The Late Precambrian fossil *Kimberella* is a mollusc-like bilaterian organism. *Nature* **388**: 868–71.
- Fike, D.A., Grotzinger, J. P., Pratt, L. M. *et al.* (2006) Oxidation of the Ediacaran ocean. *Nature* **444**:744–7.
- Fortey, R. A. and Owens, R. M. (1999) Feeding habits in trilobites. *Palaeontology* **42**:429–65.
- Fraiser, M.L., and Bottjer, D.J. (2004) The non-actualistic Early Triassic gastropod fauna: a case study of the Lower Triassic Sinbad Limestone Member. *Palaios* **19**: 259–275.
- Fraiser, M.L., Twitchett, R.J., and Bottjer, D.J. (2005) Unique microgastropod biofacies in the Early Triassic: Indicator of long-term biotic stress and the pattern of biotic recovery after the end-Permian mass extinction. *Comptes Rendus Palevol* **4**: 475–484.
- Fraiser, M.L., and Bottjer, D.J. (2007) When bivalves took over the world: *Paleobiology* **33**: 397–413.
- Fraiser, M.L., Clapham, M.E., and Bottjer, D.J. (2010) Mass extinctions and changing taphonomic processes: Fidelity of the Guadalupian, Lopingian, and Early Triassic fossil records. In: Bottjer, D.J., and Allison, P. A. (Eds.), *Taphonomy: Process and Bias Through Time*, Plenum Press.
- Galfetti, T., Bucher, H., Ovtcharova, M., *et al.* (2007) Timing of the Early Triassic carbon cycle perturbations inferred from new U-Pb ages and ammonoid biochronozones. *Earth and Planetary Science Letters* **258**: 593–604.
- Ganeshram, R. S., Calvert, S. E., Pedersen, T. F. *et al.* (1999) Factors controlling the burial of organic carbon in laminated and bioturbated sediments off NW Mexico: Implications for hydrocarbon preservation. *Geochimica et Cosmochimica Acta* **63**:1723–34.
- Gehling, J. G. (1999) Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. *Palaios* **14**:40–57.
- Gehling, J. G. (2000) Environmental interpretation and a sequence stratigraphic framework for the terminal Proterozoic Ediacara Member within the Rawnsley Quartzite, South Australia. *Precambrian Research* **100**:65–95.
- Gehling, J. G., Droser, M. L., Jensen, S. R. *et al.* (2005) Ediacara Organisms: Relating Form to Function In: *Evolving Form and Function: Fossils and Development: Proceedings of a symposium honouring Adolph Seilacher for his contributions to paleontology in celebration of his 80th birthday*. Briggs, D.E.G. (ed).
- Grard, A., François, L.M., Dessert, C., Dupré, B., and Goddérès, Y. (2005) Basaltic volcanism and mass extinction at the Permo-Triassic boundary: Environmental impact and modeling of the global carbon cycle. *Earth and Planetary Science Letters* **234**: 207–221.
- Grasby, S. E., and Beauchamp, B. (2009) Latest Permian to Early Triassic basin-to-shelf anoxia in the Sverdrup Basin, Arctic Canada. *Chemical Geology* **264**: 232–246.
- Grazhdankin, C. (2004) Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution *Paleobiology*, **30**: 203–21.
- Griffin, J.M., Marenco, P. J., Fraiser, M.L., and Clapham, M.E. (2010) Stromatolite- sponge-Tubiphites reefs in the Virgin Limestone Member of the Moenkopi Formation, Nevada: Implications for biotic recovery following the end-Permian mass extinction. *Geological Society of America Annual Meeting, Abstracts with Programs* **42**: 72.
- Grotzinger, J. P., Bowring, S. A., Saylor, B. Z. *et al.* (1995) Biostratigraphic and geochronologic constraints on early animal evolution. *Science* **270**:598–604.
- Guo, Q. F. (2007) The diversity-biomass-productivity relationships in grassland management and restoration. *Basic and Applied Ecology* **8**:199–208.
- Haas, J., Demeny, A., Hips, K., *et al.* (2006) Carbon isotope excursions and microfacies changes in marine Permian-Triassic boundary sections in Hungary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **237**: 160–181.
- Haas, J., Demeny, A., Hips, K., *et al.* (2007) Biotic and environmental changes in the Permian-Triassic boundary interval recorded on a western Tethyan ramp in the Bukk Mountains, Hungary. *Global and Planetary Changes* **55**: 136–154.
- Hays, L.E., Beatty, T., Henderson, C.M., Love, G.D., and Summons, R.E. (2007) Evidence for photic zone euxinia through the end-Permian mass extinction in the Panthalassic Ocean (Peace River Basin, Western Canada). *Palaeoworld* **16**: 39–50.

- Hotinski, K.L., Bice, L.R., Kump, R.G., Najjar, and M.A. Arthur (2001) Ocean stagnation and end-Permian anoxia. *Geology* **29**: 7–10.
- Hu, Z.W., Huang S.J., Qing, H.R., Wang, C.M., and Gao, X.Y. (2008) Evolution and global correlation for strontium isotopic composition of marine Triassic from Huaying Mountains, eastern Sichuan, China. *Science in China Series D: Earth Sciences* **51**: 540–549.
- Huang, S.J., Qing, H.R., Huang, P.P., Hu, Z.W., Wand, Q.D., Zou, M.L., and Liu, H.N. (2008) Evolution of strontium isotopic composition of seawater from Late Permian to Early Triassic based on study of marine carbonates, Zhongliang Mountain, Chongqing, China. *Science in China Series D: Earth Sciences* **51**: 528–539.
- Ieno, E. N., Solan, M., Batty, P. *et al.* (2006) How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Marine Ecology Progress Series* **311**: 263–71.
- Isozaki, Y. (1994) Superanoxia across the Permo-Triassic boundary: Record in accreted deep-sea pelagic chert in Japan. In: Embry, A.F., Beauchamp, B., Glass, D.J. (Eds.), *Pangea: Global Environments and Resources*. Canadian Society of Petroleum Geologists Memoirs **17**: 805–812.
- Isozaki, Y. (1997) Permo-Triassic boundary superanoxia and stratified superocean; records from lost deep sea. *Science* **276**: 235–238.
- Ivantsov, A.Y. (2009) New reconstruction of *Kimberella*, problematic Vendian metazoan. *Paleontological Journal* **43**: 601–11.
- Jensen, S., Droser, M. L. and Gehling, J. G. (2006) A critical look at the Ediacaran trace fossil record. In: *Neoproterozoic Geobiology and Paleobiology*. Xiao, S. and Kaufman, A. J. (eds), Springer, The Netherlands, 115–57.
- Jiang, H., Wu, Y., and Cai, C. (2008) Filamentous cyanobacteria fossils and their significance in the Permian-Triassic boundary section at Laolongdong, Chongqing. *Chinese Science Bulletin* **53**: 1871–1879.
- Kaiho, K., Chen, Z.Q., Ohashi, T., Arino, A., Swada, K., and Cramer, B.S. (2005) Negative carbon isotope anomaly associated with the earliest Lopingian (Late Permian) mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **223**: 172–180.
- Kato, Y., Nakao, K., Isozaki, Y. (2002) Geochemistry of Late Permian to Early Triassic pelagic cherts from Southwest Japan; implications for an oceanic redox change. *Chemical Geology* **182**: 15–34.
- Kaufman, A. J., Hayes, J. M. and Knoll, A. H. *et al.* (1991) Isotopic compositions of carbonates and organic carbon from upper Proterozoic successions in Namibia: stratigraphic variation and the effects of diagenesis and metamorphism. *Precambrian Research* **49**: 301–27.
- Kershaw, S., Li, Y., Crasquin-Soleau, S., Feng, Q., Mu, X., Collin, P.-Y., Reynolds, A., and Gou, L. (2007) Earliest Triassic microbialites in the South China block and other areas: Controls on their growth and distribution. *Facies* **53**: 409–425.
- Kowalewski, M., Goodfriend, G.A. and Flessa, K.W. (1998) High-Resolution Estimates of Temporal Mixing within Shell Beds: The Evils and Virtues of Time-Averaging. *Paleobiology* **24**: 287–304.
- Kidder, D.L., and Worsely, T.R. (2004) Causes and consequences of extreme Permo-Triassic warming to globally equable climate and relation to the Permo-Triassic extinction and recovery. *Palaeogeography, Palaeoclimatology, Palaeoecology* **203**: 207–238.
- Kidwell, S.M. (2002) Time-averaged molluscan death assemblages: Palimpsests of richness, snapshots of abundance. *Geology* **30**: 803–6.
- Knoll, A.H., Bambach, R.K., Payne, J.L., Pruss, S., and Fischer, W.W. (2007) Paleophysiology and end-Permian mass extinction. *Earth and Planetary Science Letters* **256**: 295–313.
- Korte, C., Kozur, H.W., Bruckschen, P., and Veizer, J. (2003) Strontium isotope evolution of Late Permian and Triassic seawater. *Geochimica et Cosmochimica Acta* **67**: 47–62.
- Krassilov, V.A., Afonin, S.A., and Baranova, S.S. (1999) *Tympanicysta* and the terminal Permian events. *Permophiles* **35**: 16–17.
- Kump, L.R., Pavlov, A.A., and Arthur, M.A. (2005) Massive release of hydrogen sulfide to the surface ocean and atmosphere during intervals of oceanic anoxia. *Geology* **33**: 397–400.
- Laflamme, M. and Narbonne, G.M.. (2008a) Ediacaran fronds. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **258**: 162–79.
- Laflamme, M., and Narbonne, G.M.. (2008b) Competition in a Precambrian world: Palaeoecology and functional biology of Ediacaran fronds. *Geology Today*, **24**: 182–7.
- Laflamme, M., Narbonne, G.M. and Anderson, M.M. (2004) Morphometric analysis of the Ediacaran frond *Charniodiscus* from the Mistaken Point Formation, Newfoundland. *Journal of Paleontology*, **78**: 827–37.
- Laflamme, M., Narbonne, G.M. and Greentree, C. *et al.* (2007) Morphology and taphonomy of the Ediacaran frond: *Charnia* from the Avalon Peninsula of Newfoundland. In: *The Rise and Fall of the Ediacaran Biota*. Vickers-Rich, P. and Komarower, P. (eds), Geological Society, London, Special Publications, **286**: 237–57.
- Laflamme, M., Schiffbauer, J.D. and Narbonne, G. M. (In press) Deep-Water Microbially Induced Sedimentary Structures (MISS) in Deep Time: The Ediacaran Fossil

- Ivesheadia*, In: *Microbial Mats in Sandy Deposits (Archean Era to Today)*, Noffke, N. K. and Chafetz, H. (eds), SEPM Special Publication.
- Laflamme, M., Schiffbauer, J.D., Narbonne, G.M. *et al.* (2011) Microbial biofilms and the preservation of the Ediacara biota. *Lethaia*, **44**: 203–13.
- Laflamme, M., Xiao, S. and Kowalewski, M. 2009. Osmotrophy in modular Ediacara organisms. *Proceedings of the National Academy of Sciences of USA* **106**: 14438–43.
- Laschet, C. (1984) On the origin of cherts. *Facies* **10**: 257–289.
- Lee, C. (1992) Controls on organic carbon preservation: The use of stratified water bodies to compare intrinsic rates of decomposition in oxic and anoxic systems. *Geochimica et Cosmochimica Acta* **56**:3323–35.
- Lehrmann, D.J. (1999) Early Triassic calcimicrobial mounds and biostromes of the Nanpanjiang Basin, South China. *Geology* **27**: 359–362.
- Liu, A.G., McLroy, D., Antcliffe, J., Brasier, M.D. (2010) Effaced preservation in the Ediacara biota and its implications for the early macrofossil record. *Palaeontology* **54**: 607–630.
- Liu, A.G., McLroy, D., Antcliffe, J., Brasier, M.D. (2011) Effaced preservation in the Ediacara biota and its implications for the early macrofossil record. *Palaeontology* **54**: 607–630. Logan, G.A., Hayes, J.M., Hieshima, G.B. *et al.* (1995) Terminal Proterozoic reorganization of biogeochemical cycles. *Nature* **376**: 53–7.
- Loreau, M., Naeem, S., Inchausti, P. *et al.* (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–8.
- Marenco, K.N., and Bottjer, (2011) Quantifying bioturbation in Ediacaran and Cambrian rocks. In: *Quantifying the Evolution of Early Life: Numerical Approaches to the Evaluation of Fossils and Ancient Ecosystems, Topics in Geobiology Series*, Laflamme, M., Schiffbauer, J.D. and Dornbos, S.Q. (eds), **36**:135–60, Springer, Dordrecht.
- Marinelli, R. L., and Williams, T. J. (2003) Evidence for density dependent effects of infauna on sediment biogeochemistry and benthic-pelagic coupling in nearshore systems. *Estuary and Coastal Shelf Science* **57**:179–92.
- McLroy, D. and Logan, G. A. (1999) The impact of bioturbation on infaunal ecology and evolution during the Proterozoic–Cambrian transition. *Palaaios* **14**: 58–72.
- Mermillod-Blondin, F., François-Carcaillet, F. and Rosenberg, R. (2005) Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: an experimental study. *Journal of Experimental Marine Biology and Ecology* **315**:187–209.
- Mittelbach, G. G., Steiner, C. F., Scheiner, S. M. *et al.* (2001) What is the observed relationship between species richness and productivity? *Ecology* **82**:2381–96.
- Naeem, S. (1998) Species redundancy and ecosystem reliability. *Conservation Biology*. **12**:39–45.
- Naeem, S. (2002) Disentangling the impacts of diversity on ecosystem functioning in combinatorial experiments. *Ecology* **83**:2925–35.
- Narbonne, G. M. (2004) Modular construction of Early Ediacaran complex life forms. *Science*, **305**:1141–4.
- Narbonne, G. M. (2005) The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annual Review of Earth and Planetary Sciences* **33**:421–42.
- Narbonne, G. M., Laflamme, M., Greentree, C. *et al.* (2009) Reconstructing a lost world: Ediacaran rangeomorphs from Spaniard's Bay, Newfoundland. *Journal of Paleontology* **83**:503–523.
- Nielsen, J., and Shen, Y. (2004) Evidence for sulfidic deep water during the Late Permian in the East Greenland Basin. *Geology* **32**: 1037–1040.
- Norling, K., Rosenberg, R., Hulth, S. *et al.* (2007) Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series* **332**:11–23.
- Ogg, J.G., Ogg, G., and Gradstein, F.M. (2008) *The Concise Geologic Time Scale*. Cambridge University Press, 150 pp.
- Payne, J. L., and Finnegan, S. (2006) Controls on marine animal biomass through geological time. *Geobiology* **4**: 1–10.
- Payne, J.L., and Kump, L.R. (2007) Evidence for recurrent Early Triassic massive volcanism from quantitative interpretation of carbon isotope fluctuations. *Earth and Planetary Science Letters* **256**: 264–277.
- Payne, J. L., and van de Schootbrugge, B. (2007) Life in Triassic oceans: Links between planktonic and benthic recovery and radiation. 165–189. In Falkowski, P.G., and Knoll, A.H. (Eds.), *Evolution of Primary Producers in the Sea*. Academic Press.
- Payne, J.L., Lehrmann, D.J., Wei, J., and Knoll, A.H. (2006) The pattern and timing of biotic recovery from the end-Permian extinction of the Great Bank of Guizhou, Ghizhou Province, China. *Palaaios* **21**: 63–85.
- Paytan, A., and Griffith, E. M. (2007) Marine barite: recorder of variations in ocean export productivity. *Deep Sea Research Part II: Topical Studies in Oceanography* **54**:687–705.
- Pell, S. D., McKirdy, D. M., Jansyn, J. *et al.* (1993) Ediacaran carbon isotope stratigraphy of South Australia—an initial study. *Transactions of the Royal Society of South Australia* **117**:153–61.
- Petchey O. L., and Gaston, K. J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters* **5**:402–11.

- Petchey O. L. and Gaston, K. J. (2005) Extinction and the loss of functional diversity. *Proceedings of the Royal Society of London, B* **269**:1721–7.
- Petchey, O. L., Hector, A. and Gaston, K. J. (2004) How do different measures of functional diversity perform? *Ecology* **85**:847–57.
- Piper, D. Z., and Calvert, S. E. (2009) A marine biogeochemical perspective on black shale deposition. *Earth-Science Reviews* **95**:63–96.
- Piper, D. Z., and Perkins, R. B. (2004) A modern vs. Permian black shale—the hydrography, primary productivity, and water-column chemistry of deposition. *Chemical Geology* **206**:177–97.
- Plotnick, R.E., Dornbos, S.Q. and Chen, J.Y. (2010) Information landscapes and the sensory ecology of the Cambrian radiation. *Paleobiology* **36**: 303–17.
- Pomeroy, L.R., Williams, P.J.I., Azam, F. *et al.* (2007) The microbial loop. *Oceanography* **20**: 28–33.
- Pruss, S.B., Bottjer, D.J., Corsetti, F.A., and Baud, A. (2006) A global marine sedimentary response to the end-Permian mass extinction: Examples from southern Turkey and the western United States. *Earth-Science Reviews* **78**: 193–206.
- Racki, G. (1999) Silica-secreting biota and mass extinctions: Survival patterns and processes. *Palaeogeography, Palaeoclimatology, Palaeoecology* **154**: 107–132.
- Rampino, M.R., and Caldeira, K. (2005) Major perturbation of ocean chemistry and a ‘Strangelove Ocean’ after the end-Permian mass extinction. *Terra Nova* **17**: 554–559.
- Raup, D.M., and Sepkoski, J.J. (1982) Mass extinctions in the marine fossil record. *Science* **215**: 1501–1503.
- Riccardi, A., Kump, L.R., Arthur, M.A., and D’Hondt, S. (2007) Carbon isotopic evidence for chemocline upward excursions during the end-Permian event. *Palaeogeography, Palaeoclimatology, Palaeoecology* **248**: 73–81.
- Riding, R. (2000) Microbial carbonates: The geological record of calcified bacterial-algal mats and biofilms. *Sedimentology* **47**: 179–214.
- Rosenzweig, M. L. and Z. Abramsky. (1993) How are diversity and productivity related? Pp. 52–65 In: *Species Diversity and Ecological Communities*. Ricklefs, R. E. and Schluter, D. (eds), University of Chicago Press, Chicago.
- Rothman, D.H., Hayes, J.M. and Summons, R.E. (2003) Dynamics of the Neoproterozoic carbon cycle: *Proceedings of the National Academy of Sciences* **100**:8124–9.
- Sedlacek, A.R.C., Saltzman, M.R., and Linder, J.S. (2008) The Permian-Triassic boundary in the western United States. *Geological Society of America, Annual Meeting Abstracts and Programs*, Houston.
- Seilacher, A. (1992) Vendobionta and Psammocorallia: lost constructions of Precambrian evolution. *Journal of the Geological Society, London* **149**: 607–13.
- Seilacher, A. (1999) Biomat-related lifestyles in the Precambrian. *Palaios* **14**:86–93.
- Seilacher, A., Buatois, L. A. and Mángano, M. G. (2005) Trace fossils in the Ediacaran-Cambrian transition: behavioral diversification, ecological turnover and environmental shift. *Palaeogeography, Palaeoclimatology, Palaeoecology* **227**:323–56.
- Seilacher, A., and Pflüger, F. (1994) From biomats to benthic agriculture: a biohistoric revolution. *Biostabilization of sediments*. In: Krumbein, W. E., Paterson, D. M. and Stal, L. J. (eds), Bibliotheks und Informationssystem der Universität Oldenburg, Oldenburg, 97–105.
- Sephton, M.A, Looy, C.V., Brinkhuis, H., Wignall, P.B., de Leeuw, J.W., Visscher, H. (2005) Catastrophic soil erosion during the end-Permian biotic crisis. *Geology* **33**: 941–944.
- Servais, T., Owen, A. W., Harper, D. A. T., Kröger, B. R., and Munnecke, A. (2010) The Great Ordovician Biodiversification Event (GOBE): The palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology* **294**: 99.
- Sheehan, P. (1996) A new look at Ecologic Evolutionary Units (EEUs). *Palaeogeography, Palaeoclimatology, Palaeoecology* **127**: 21–32.
- Sheldon, N.D. (2006) Abrupt chemical weathering increase across the Permian-Triassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **231**: 315–321.
- Shen, B., Dong, L., Xiao, S.H. and Kowalewski, M. (2008) The Avalon explosion: evolution of Ediacara morphospace. *Science* **319**:81–4
- Solan, M., P. Batty, Bulling, M. T. and Godbold, J. A. (2008) How biodiversity affects ecosystem processes: implications for ecological revolutions and benthic ecosystem function. *Aquatic Biology* **2**:289–301.
- Solan, M., Cardinale, B. J., Downing, A. L. *et al.* (2004) Extinction and ecosystem function in the marine benthos. *Science* **306**:1177–80
- Sperling, E.A., Ingle, J.C., Jr. (2006) A Permian-Triassic boundary section at Quinn River Crossing, northwestern Nevada, and implications for the cause of the Early Triassic chert gap on the western Pangean margin. *Geological Society of America Bulletin* **118**: 733–746.
- Sperling, E.A., Peterson, K.J. and Laflamme, M. (2011) Rangeomorphs, *Thectardis* (Porifera?) and dissolved organic carbon in the Ediacaran ocean. *Geobiology*, **9**: 24–33.
- Sperling, E.A., Pisani, D. and Peterson, K.J. (2007) Poriferan paraphyly and its implications for Precambrian palaeobiology. In: *The Rise and Fall of the Ediacaran Biota*, Vickers-Rich P, Komarower P (eds), *Geological Society of London, Special Publications* **286**: 355–68.

- Sperling, E.A. and Vinther, J. (2010) A placozoan affinity for Dickinsonia and the evolution of late Proterozoic metazoan feeding modes. *Evolution and Development* **12**:201–9.
- Suzuki, N., Ishida, K., Shinomiya, Y., and Ishiga, H. (1998) High productivity in the earliest Triassic ocean: Black shales, southwest Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology* **141**: 53–65.
- Takahashi, S., Oba, M., Kaiho, K., Yamakita, S., and Sakata, S. (2009) Panthalassic oceanic anoxia at the end of the Early Triassic: A cause of delay in the recovery of life after the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **274**: 185–195.
- Takemura, A., Aita, Y., Sakai, T., Kamata, V., Suzuki, N., Iiori, R.S., Famakita, S., Sakakibara, M., Campbell, H., Fujiki, T., Ogane, K., Takemura, S., Sakamoto, S., Kodama, A., and Nakamura, Y. (2003) Conodont-based age determination for a radiolarian-bearing Lower Triassic chert sequence in Arrow Rocks, New Zealand. *Tenth Meeting of the International Association of Radiolarian Palaeontologists, Abstracts and Programs*, University of Lausanne.
- Thayer, C. W. (1979) Biological bulldozers and the evolution of marine benthic communities. *Science* **203**:458–61.
- Thayer, C.W. (1983) Sediment-mediated biological disturbance and the evolution of marine benthos. In: Tevesz, M.J.S., McCall, P.L. (Eds.), *Biotic Interactions in Recent and Fossil Communities*. Plenum Press, New York: 479–625.
- Thomas, B. M., Willink, R. J., Grice, K., Twitchett, R. J., Purcell, R. R., Archbold, N. W., George, A. D., Tye, S., Alexander, R., Foster, C. B. and Barber, C. J. (2004) Unique marine Permian–Triassic boundary section from Western Australia. *Australian Journal of Earth Sciences* **51**: 423–430.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- Tilman, D., Knops, J., Wedin, D. *et al.* (1997) The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300–2.
- Tomašovič A., and Kidwell, S.M. (2010) Predicting the effects of increasing temporal scale on species composition, diversity, and rank-abundance distributions. *Paleobiology* **36**:672–95.
- Trappe, J. (1994) Pangean phosphorites-ordinary phosphorite genesis in an extraordinary world? *Pangea: Global Environments and Resources, Canadian Society of Petroleum Geologists* **17**: 469–478.
- van Ruijven, J., and Berendse, F. (2005) Diversity-productivity relationships: initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences, USA* **102**:695–700.
- Waggoner, B. (2003) The Ediacaran biotas in space and time. *Integrative and Comparative Biology* **43**:104–13.
- Wagner P.J., Kosnik, M.A., and Lidgard S. (2006) Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. *Science* **314**: 1289–1292.
- Waide, R. B., Willig, M. R., Steiner, C. F. *et al.* (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* **30**:257–3000.
- Wignall, P.B. and Twitchett, R.J. (1996) Oceanic anoxia and the end Permian mass extinction. *Science* **272**: 1155–1158.
- Wilby, P.R., Carney, J.N. and Howe, M.P.A. (2011) A rich Ediacaran assemblage from eastern Avalonia: Evidence of early widespread diversity in the deep ocean. *Geology* **39**: 655–8.
- Winguth, A.M.E., and Maier-Reimer, E. (2005) Causes of marine productivity and oxygen changes associated with the Permian-Triassic boundary: A re-evaluation with ocean general circulation models. *Marine Geology* **217**: 283–304.
- Whittington, H.B. and Briggs, D.E.G. (1985) The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London* **309**: 569–609.
- Wood, D. A., Dalrymple, R.W., Narbonne, G. M. *et al.* (2003) Palaeoenvironmental analysis of the late Neoproterozoic Mistaken Point and Trepassey formations, southeastern Newfoundland. *Canadian Journal of Earth Sciences* **40**:1375–139.
- Worm, B. and Duffy, J. E. (2003) Biodiversity, productivity, and stability in real food webs. *Trends in Ecology and Evolution* **18**:628–32.
- Worm, B., Lotze, H. K., Hillebrand, H. *et al.* (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature* **417**:848–51.
- Xiao, S. and Laflamme, M. (2009) On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends in Ecology and Evolution* **24**:31–40.
- Xie, S., Pancost, R.D., Yin, H., Wang, H., and Evershed, R.P. (2005) Two episodes of microbial change coupled with Permo/Triassic faunal mass extinction. *Nature* **434**: 494–497.
- Zhao, F., Caron, J.B., Hu, S.X. *et al.* (2009) Quantitative analysis of taphofacies and paleocommunities in the early Cambrian Chengjiang Lagerstätte. *Palaios* **24**: 826–39.