11
PLANTS AND ANIMALS AS GEOBIOLOGICAL AGENTS

David J. Beerling[1] and Nicholas J. Butterfield[2]

[1]Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
[2]Department of Earth Sciences, University of Cambridge, Cambridge, CB2 2EQ, UK

11.1 Introduction

Unlike the world of prokaryotes and protists, plants and animals have a relatively limited metabolic repertoire – essentially oxygenic photoautotrophs or aerobic heterotrophs – but they make up for this shortfall through their enormous, seemingly inexhaustible, capacity to exploit morphology. Plants and animals are unique in having independently acquired a tissue and organ-grade level of multicellularity, thereby taking intra-organismal divisions of labour to fundamentally new levels, not least the invention of large size, complex life histories and complex behaviour. Morphological, metabolic and tissue chemistry developments, therefore, collectively open doors to entirely novel approaches for exploiting ecospace, which in turn exert major influences on global biogeochemical cycles and the environment.

One of the most direct and effective means of assessing the role of plants and animals as geobiological agents is to examine evidence for the expression of these effects on geological and evolutionary timescales (i.e. over millions of years). The geological record offers a unique view of ancient conditions and alternative worlds, including those partially or entirely devoid of the modern complement of plants and animals. In this chapter, we review the influence of terrestrial plants and animals on the physical and biological processes affecting the Earth system. Insofar as the record of land plants appears to extend no further than the Ordovician (Wellman *et al.*, 2003), and eumetazoans no further than the Ediacaran (Peterson and Butterfield, 2005), this review is limited to the relatively recent past (ca. 635 million years), though comparison with pre-embryophyte- and

pre-eumetazoan-worlds offers a powerful insight into the progressive geobiological impact of these two remarkable clades.

11.2 Land plants as geobiological agents

The geobiological activities of plants and vegetation operate on short (minutes to year) and very long (millions of years) timescales. On short timescales, they alter the energy balance of the landscape and the chemistry of atmospheric greenhouse gases and their precursors, as well as affecting the atmospheric loading of organic aerosols (e.g. Tunved *et al.*, 2006; Claeys *et al.*, 2004; Spracklen *et al.*, 2008). On longer timescales, plants' geobiological actions are expressed by their accumulated influence on the operation of the organic and inorganic carbon cycles. Here, the net effects are on global atmospheric O_2 and CO_2 levels respectively, with an influence on the evolutionary trajectory of Earth's climate and terrestrial biota (Berner, 2004; Beerling, 2007).

11.2.1 Short-term feedback processes (10^0 to 10^3 years)

11.2.1.1 Land surface energy balance

Terrestrial vegetation, especially forests and grasslands, control the exchange of water, energy and momentum between the land surface and the atmosphere (Bonan, 2008). Ecosystems can therefore exert geobiophysical forcings and feedbacks that dampen or amplify regional and global climate change. In turn these effects also play a role in determining the structure, function and distribution of vegetation. Albedo and evapotranspiration

(canopy transpiration + soil evaporation) are two key ecosystem processes influencing land surface energy budgets. The global energy budget is given by the simple energy balance equation (Crowley and North, 1991):

$$\frac{S_c}{4(1-\alpha)} = \varepsilon \sigma T^4 \tag{11.1}$$

where S_c is the solar constant (1367 W m^{-2} at 0 Ma), σ is the planterary albedo (viewed from the top of the atmosphere), ε is the planetary emissivity, i.e. capacity to emit long-wave radiation, and σ is the Stefan–Boltzman constant (5.67×10^{-8} W m^{-2} K^{-4}), and T is planetary temperature (K). The division of S_c by 4 accounts for the fact that the Earth absorbs radiation like a two dimensional disc, but in fact this is spread over the surface area of a sphere (because of the Earth's rotation) which has four surface area of times the area of a disk. Equation 11.1 can be modified to be more relevant to terrestrial ecology and predict mean terrestrial surface temperature from incoming solar energy, albedo and atmospheric CO_2, as discussed by Beerling and Woodward (2001).

Terrestrial albedo depends primarily on vegetation type and the leaf area index (LAI), the number of leaf layers in the canopy, a trait which can vary seasonally depending on climate and the dominant functional type of vegetation. Incoming solar energy absorbed by the canopy is dissipated by evaporation (latent heat) or convective radiation (sensible heat). Evaporation of water from plant canopies and soils therefore increases the flux of latent heat from the land surface. In tropical rainforests of Amazonia, for example, about 80% of the intercepted net radiation is dissipated as latent heat and 20% lost by convection (Grace *et al.*, 1995). Vegetation height also influences local climate by changing the degree of aerodynamic coupling between the land surface and the atmosphere; taller trees are aerodynamically rougher, enhancing the transfer of mass and energy through increased turbulence.

Soil water content plays a critical role in regulating ecosystem evapotranspiration. As the soils dries out, and the moisture zone around roots is depleted, stomatal pores on the surface of leaves close, reducing transpirational cooling by latent heat loss (Buckley, 2005). This, in turn, leads to elevated canopy temperatures with greater upwards transport of sensible heat to the atmosphere, to an extent governed by the surface-to-air temperature gradient.

The maximum influence of these vegetation properties on global climate has been assessed by comparing climate model simulations between two hypothetical extremes, 'desert world' and a 'green world' (Kleidon *et al.*, 2000). Desert world is characterized by a smooth land surface with a high albedo and poor soil water storage capacity, whereas a green world with forests everywhere has the opposite characteristics. In this extreme comparison, vegetation tripled land surface evapotranspiration, enhanced atmospheric moisture and cloud cover leading to a doubling of land-surface precipitation. These effects combined to lower near-surface seasonal mean temperatures by 8 K in the 'green world' simulation compared that of 'desert world'. In the context of these idealized calculations, the net cooling effect of vegetation indicates its effects on the hydrological cycle overwhelm any increased net absorption of radiation at the surface due to a lower albedo compared to deserts (Kleidon *et al.*, 2000).

In real deserts, the absence of vegetation feedbacks is proposed to promote their own existence (Charney, 1975; Charney *et al.*, 1975). Deserts are stable entities because their sandy non-vegetated surfaces reflect solar radiation back to space, effectively allowing them to act as a net heat sink relative to surrounding areas, which in turn cools the air above. This cooling draws airflow inwards over the Sahara, which warms and dries as it descends, greatly reducing the chances of rainfall and the establishment of vegetation.

Palaeoclimate modelling studies quantifying the importance of vegetation-climate interactions are generally restricted to the Cretaceous, with more comprehensive studies focusing on vegetation feedbacks in a future 'greenhouse' world (e.g. Sellers *et al.*, 1996; Betts *et al.*, 1997). In the warm Late Cretaceous environment (80–65 Ma ago), forest distribution was extensively modified compared to the present-day situation, notably by their extending throughout the high northern and southern latitude continental land masses (Upchurch *et al.*, 1998; Beerling and Woodward, 2001). Climate modelling indicates that the presence of high-northern latitude deciduous forests warmed January and July land-surface temperatures by 2–4 °C and up to 8 °C, respectively, compared to simulations with bare-ground or tundra (Otto-Bliesner and Upchurch, 1997; Upchurch *et al.*, 1998; DeConto *et al.*, 2000). The wintertime warming occurs because the trees mask snow cover, decreasing the albedo of the land surface. Some of the warming is advected to the nearby high-latitude oceans and initiates sea-ice loss (Otto-Bliesner and Upchurch, 1997; Upchurch *et al.*, 1998). Nevertheless, even after accounting for vegetation-land surface feedbacks, reproducing the warm wintertime continental climates of past greenhouse eras in the current generation of climate models, and even next generation 'Earth systems' models, continues to remain a major challenge and implies key processes are missing or poorly represented.

Investigations of the direction and magnitude of vegetation-climate feedbacks in a future high CO_2 'greenhouse' world reveal a more complex picture with competing physiological and structural feedbacks (Sellers *et al.*, 1996; Betts *et al.*, 1997). Doubling the atmospheric CO_2 concentration could decrease in stomatal

conductance of vegetation (Ainsworth and Rogers, 2007), with attendant reductions in transpiration and possible warming through a decreased latent heat flux. Global simulations characterising this 'physiological feedback' effect suggest widespread warming over the northern hemisphere land surface by 1 °C (Betts *et al.*, 1997). However, a CO_2-rich atmosphere could also alter vegetation structural properties, like LAI, by stimulating photosynthetic and water-use efficiency of growth (Ainsworth and Long, 2005; Ainsworth and Rogers, 2007). This structural response of vegetation to CO_2 could largely offset the warming effects of physiology by increasing evapotranspiration with a greater LAI and total canopy conductance to water vapour (Betts *et al.*, 1997). The net sign of the feedback of predicted changes in vegetation physiology and structure in a near-term future (i.e. decades), without significant migration of biomes under high CO_2 atmosphere is likely to be a cooling. However, climate-carbon cycle simulations indicate that significant afforestation of the high latitudes, often proposed as a measure to counteract global warming, may be counter-productive leading to warming through decreases in land surface albedo (Bala *et al.* 2007). Analyses of this sort raise questions concerning the efficacy of such efforts to mitigate climate change.

Recent evidence from the high arctic suggests vegetation is already exerting an effect on climate through changing the land surface albedo. Accelerated warming over the high-latitude northern continents has reduced seasonal snow cover shifting the albedo of the landscape from very reflective snow to the darker underlying vegetation and soils (Chapin *et al.*, 2005). The darker vegetation absorbs more solar radiation, warming the land surface and heating the atmosphere. At the same time, rapid vegetation change is also evident, with tree and shrub expansion into more northerly regions replacing low-lying tundra ecosystems (Chapin *et al.*, 2005; Sturm *et al.*, 2005), with a profound significance for regional climatic warming by increased heat transfer to the atmosphere (Strack *et al.*, 2007).

We emphasize that our understanding of 'geobiological' feedbacks of vegetation for past or future climates and atmospheres is largely derived from theory, applied and embedded in large complex computer models. Evaluating models against palaeobotanical, geochemical and sedimentary evidence is therefore a critical endeavour.

11.2.1.2   Atmospheric composition and aerosols

Greenhouse gases in the atmosphere absorb long-wave radiant energy emitted from the Earth's surface rather than letting it escape into space. On geological timescales, terrestrial ecosystems influence the atmospheric CO_2 concentration by accelerating weathering of Ca-Mg

rocks and to lesser extent through organic carbon burial (see next section). On human timescales vegetation plays an important role in modulating anthropogenic CO_2 emissions from fossil fuel burning and deforestation. Net primary productivity (NPP) is defined as the uptake of CO_2 by photosynthesis less that released by autotrophic (plant) respiration. This primary production provides the energy sources and substrates for virtually all major ecosystems on Earth. Net ecosystem productivity is NPP less carbon lost by decomposition via heterotrophic (microbial and fungal) respiration. In addition, organic carbon is also lost through disturbance by, for example, fire. At the global scale, terrestrial NPP today is about 60 Pg C yr^{-1}, comparable to that of the ocean biosphere (65 Pg C yr^{-1}) (Falkowski *et al.*, 1998). Accounting for heterotrophic respiration reduces NPP considerably to about 5 Pg C yr^{-1}, and allowing for carbon losses by disturbances such as fire and soil erosion lowers it further to about 2–3 Pg C yr^{-1}. This carbon sink is small but of a similar magnitude to annual emissions due to humanity's burning of fossil fuels and deforestation (9 Pg yr^{-1}) (Woodward, 2007). Vegetation therefore represents an important sink for about 20–30% of human emissions to an extent that varies from year to year due to climatic variability. Because atmospheric CO_2 is well-mixed globally, vegetation–carbon cycle feedbacks are usually manifested globally whereas the land surface biophysical feedbacks discussion occur most strongly at regional scales.

Terrestrial ecosystems play an important role in determining atmospheric concentrations of the three important trace greenhouse gases, methane (CH_4), ozone (O_3) and nitrous oxide (N_2O) in the lower atmosphere (troposphere) (Beerling *et al.*, 2007). Collectively these trace greenhouse gases are fundamentally important components of the global climate system. On a per molecule basis, for example, methane and ozone are approximately 25 and 1000 times, respectively, more effective at planetary warming than CO_2 over a 100-year timeframe but are present in far lower concentrations. Biogenic sources of methane also lead to indirect climatic warming because atmospheric methane oxidation supplies the relatively dry lower stratosphere with water vapour, where it acts as a very effective greenhouse gas.

Terrestrial ecosystems are the largest natural sources of methane and nitrous oxide and therefore strongly influence the concentrations of both gases in the lower atmosphere. The activities of methane-producing Archaea (methanogens) in anaerobic natural wetland soils supply about 200 Tg CH_4 annually, while microbial activities in the soils of tropical and temperate forests annually release about 10 Tg N_2O. Soil microbial activity, particularly in the tropics and sub-tropics, also release nitrogen oxides (NO_x = NO and NO_2) (5–8 Tg yr^{-1}), with further emissions from biomass/biofuel burning

(ca. 6–12 Tg yr^{-1}) and lightning (ca. 3–7 Tg yr^{-1}) (Denman *et al.*, 2007). NO$_x$ is an important atmospheric constituent for many key chemical reactions and its production by terrestrial ecosystems, either directly or indirectly, in a preindustrial atmosphere prior to anthropogenic sources, highlights another important indirect geobiologial influence of vegetation.

Polar ice core records of Earth's past atmospheric composition indicate that the concentration of both methane and nitrous oxide underwent significant variations on glacial-interglacial timescales, as well as on millennial timescales since the last glacial epoch, some 20 kyr ago (Flückiger *et al.*, 2004). In contrast with atmospheric CO$_2$, these variations are in phase with temperature, indicating the high sensitivity of the sources of methane and nitrous oxide to climate change. Further back in Earth's history, during much of the Mesozoic and early Palaeogene, climates were considerably warmer than even the warmest interglacial climate (Huber *et al.*, 2000; Beerling and Woodward, 2001). It follows, therefore, that past greenhouse climates, characterized by a more vigorous hydrological cycle due to largely ice-free polar regions, and warmer temperatures, offer conditions expected to enhance methane and nitrous oxide emissions from terrestrial ecosystems. It is likely, therefore, that the concentration of methane and nitrous oxide in the atmosphere at these times far exceeded levels for which we have direct measurements or experience, with significant climate change potential.

Forests also alter the chemistry of the atmosphere by releasing biogenic volatile organic compounds (BVOC) (Fehsenfeld *et al.*, 1992). Isoprene is the most reactive BVOC, with a chemical lifetime ranging from a few minutes to hours. At the global scale, the terrestrial biosphere annually emits 500–750 Tg yr^{-1} of isoprene (Guenther *et al.*, 2006), over double the mass of methane produced by natural wetlands. Isoprene is an important natural precursor for the formation of tropospheric ozone, when oxidized by hydroxyl radicals in the presence of sufficient NO$_x$. Because the principal sink for methane is oxidation by hydroxyl radicals, BVOC emissions from forests can alter the lifetime and concentration of methane and its potential for planetary warming. BVOCs constitute only 1% of the total carbon flux into the atmosphere, yet act as significant drivers of climate change by influencing the photochemistry of methane and ozone, and the formation of secondary organic aerosols (SOAs) in the atmosphere.

Secondary organic aerosols arise when the oxidation products of BVOCs, especially monoterpene emitted from vegetation, condense on existing aerosol particles, and can be an important component of the aerosol loading of the atmosphere in many regions of the globe. Newly formed particles can grow rapidly to gain a diameter >70 nm and act as effective cloud condensation nuclei (CCN) (Claeys *et al.*, 2004). Aerosols influence climate both directly by scattering and absorbing incoming solar radiation and indirectly by forming CCN which influence a range of cloud properties, including albedo, lifetime, and precipitation efficiency (Spracklen *et al.*, 2008). Above northern European boreal forests, BVOCs emitted in late spring and early autumn contribute to 12–50% of the aerosol mass and sustain CCN of 200 cm^{-3}, double that of maritime air masses (Tunved *et al.*, 2006), whilst over the Amazonian rainforest photo-oxidation of isoprene produces considerable quantities of SOA, with important implications for the radiation budget (Claeys *et al.*, 2004). The magnitude and sign of terrestrial, and marine (Kump and Pollard, 2008), aerosol-cloud feedbacks during warm, high CO$_2$ pre-Quaternary climates are at very early stages of investigation.

11.2.1.3 Evolving short-term geobiological feedbacks

The capacity of vegetation land surfaces to alter the physical and chemical environment of the Earth system through this suite of processes is likely to have been most strongly exerted during the early evolutionary diversification of terrestrial plants between the Ordovician and Devonian (450–360 Ma ago). Initial stages of land colonization were conducted by primitive shallow-rooting non-vascular plants during the Ordovician (470–450 Ma ago), and were followed by small rhizomatous vascular plants in the late Silurian and early Devonian. The shallow-rooting, coarse, hairless root structures, of these plants, together with their dependency on homospory for reproduction, confined them to heterogeneous patches in lowland habitats. By the Late Devonian (385–360 Ma ago), the appearance of arborescence vegetation reaching heights of 30 m, and the development of seed habit, allowed colonization of a broader range of environments including uplands and primary successional habitats (Algeo and Scheckler, 1998). Reproduction by seed was a key factor in the rapid spread and diversification of ancient gymnosperm forests during the Late Devonian and Early Carboniferous. Rapid increases in vegetation height were associated with the development of deeper and more complex rooting systems penetrating up to 1 m into the regolith (Algeo and Scheckler, 1998; Raven and Edwards, 2001).

The spread and diversification of the above-ground terrestrial biomass in the form of deep-rooting trees and forests, likely strengthened several feedbacks with opposing signs. The two primary warming effects would be exerted through decreased land surface albedo and the evolution of methane-emitting wetland ecosystems. Counteracting such effect might be the competing with cooling effects from increasing rates of evapotranspiration

and cloud cover. The sign of biological aerosol-cloud feedbacks remains to be assessed. Compared to the algal and cyanobacterial mats that existed prior to the Ordovician, the lowering of continental albedo as forests expanded their geographical distributions which could have enhanced atmospheric heating, particularly in the high latitudes where the potential for masking seasonal snow cover is greatest. The evolution and spread of persistent floras in a diversity of wetland habitats (Greb *et al.*, 2006) would have increased methane emissions raising tropospheric concentrations to those approaching the contemporary atmosphere, with exceptionally high levels predicted during the Carboniferous when peat-forming plant communities were geographically very extensive (Bartdorff *et al.*, 2008; Beerling *et al.*, 2009). The taxonomic distribution of extant isoprene emitting groups of plants is broad, and includes mosses and gymnosperms (Sharkey *et al.*, 2008), implying that an expanding biomass increased emissions of isoprene and other BVOCs, with possible increases in methane lifetime and concentration by reduced hydroxyl radical concentrations. If wildfires produced sufficient NO_x in the Palaeozoic (Scott and Glasspool, 2006), increased isoprene emissions may have also increased tropospheric ozone concentrations, causing further warming.

Countering any warming effects from these processes, an expanding cover, density and height of vegetation, and deepening of the soil profile, throughout the Palaeozoic would have permitted a more vigorous hydrological cycle, greater rates of evapotranspiration and cloud formation. In addition, a greater atmospheric loading of biological VOCs may also have increased SOA formation over these ancient forested ecosystems, inducing further seasonal cooling both by reflecting incoming short-wave radiation back to space and by seeding cloud formation. All of these geobiological feedbacks remain to be investigated and quantified.

11.2.2   Long-term feedback processes ($>10^6$ years)

Operating in parallel with the processes described above are the geobiological activities of plants that, when summed over millions of years, influence atmospheric O_2 and CO_2 levels (Berner, 2004; Beerling, 2007). Oxygen is a physiologically important gas, and therefore substantial fluctuations in the past are implicated in altering biotic evolutionary trajectories.

11.2.2.1   Organic carbon cycle, atmospheric oxygen and biotic evolution

The organic carbon cycle involves the conversion of inorganic (atmospheric) CO_2 to plant biomass via photosynthesis, and the burial of that organic matter in sediments preventing its decomposition by consumption of

oxygen. Carbon burial leads to the net addition of O_2 to the atmosphere and is reversed when sediments and rocks are uplifted or exposed by falling sea-levels to allow oxidation of the organic matter. Only when organic matter is buried and prevented from decomposing can O_2 accumulate in the atmosphere. Rates of organic matter burial therefore significantly determine the Earth's O_2 content over millions of years (Berner and Canfield, 1989).

On an annual time-step, O_2 production by photosynthesis and O_2 consumption by heterotrophic organisms (i.e. those that acquire carbon from other organic matter rather than synthesizing it themselves) are finely balanced; only about 1% of photosynthesized organic carbon is actually buried. The overall process is represented by the following global equation:

$$CO_2 + H_2O \leftrightarrow CH_2O + O_2 \qquad (11.2)$$

Moving from left to right, Equation 11.2 shows inorganic carbon (CO_2) fixed by net photosynthesis being converted to organic matter (CH_2O) that becomes buried in sediments, releasing O_2. The reverse reaction, in Equation 11.2 represents the two processes of oxidation of old sedimentary organic matter subjected to chemical weathering on continents, and the thermal breakdown of organic matter. Both processes release reduced carbon compounds and lead to its oxidation, consuming O_2.

Organic carbon burial occurs on land most obviously in tropical or temperate mires, or peatland ecosystems, where the anoxic sedimentary environment retards decomposition by aerobic heterotrophic microbes. The evolutionary appearance, spread and diversification of land plants during the mid- to late-Palaeozoic (440–255 Ma ago) massively increased organic carbon production and burial worldwide both on land and at sea (Berner and Canfield, 1989; Robinson, 1990a,b; Berner *et al.*, 2003a). Enhanced carbon burial during this interval in Earth's history was probably linked to three factors: (i) increased terrestrial biomass, (ii) the evolutionary appearance of lignin, a microbially resistant compound plants adopted for structural integrity, and (iii) physical aspects of the depositional environment favouring the appearance of coal swamp habitats including tectonism, expansive epicontinental seas and wet climates (Berner and Canfield, 1989; Robinson, 1990a,b).

Marine burial of terrestrially derived organic carbon in anoxic muds of continental margins occurs when rainfall on continental surfaces flushes soil minerals loaded with organic matter out to sea. Burial efficiency of the organically-coated particles on continental margins is dependent on sedimentation rate. The Bengal fan system, for example, has a high organic carbon burial efficiency because the high erosion rate in the Himalayas generates high sedimentation rates and low oxygen

Figure 11.1 Schematic representation of the long-term carbon cycle.
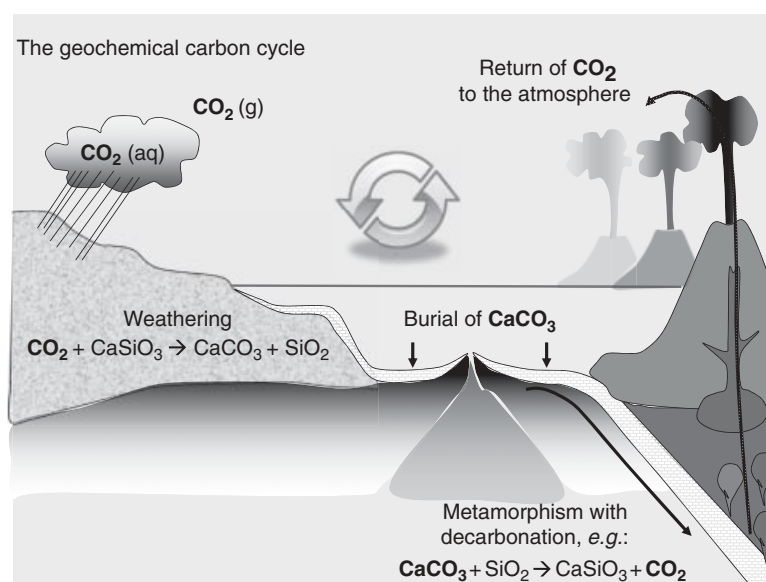
availability (Galy *et al.*, 2007). In contrast, the Amazon basin experiences far lower sedimentation rates and 70% of the riverine organic carbon is returned to the atmosphere before burial in marine sediments (Hedges *et al.*, 1997).

Geochemical models of the Earth's oxygen cycle simulating changes in the organic carbon and sulphur cycles over the Phanerozoic predict the consequences for Earth's atmospheric O_2 concentration (Berner and Canfield, 1989; Berner, 2004). The burial and weathering of sulphur is included because it influences atmospheric O_2 over geological time, though quantitatively it is less significant than the role of organic carbon. Although aspects of the calculations are uncertain, geochemical models consistently predict that O_2 levels rose to a peak value of ~27–35% during the Permo-Carboniferous (centred at around 300 Ma ago), driven chiefly by the enhanced burial of terrestrial and marine organic debris worldwide. Atmospheric O_2 concentrations then fell over the following 50 Ma to an unprecedented low of ~13–15% during the late Permian and early Triassic (250 Ma ago), when continental uplift and climatic drying reduced the geographical extent of lowland forests and swamps, reducing burial of organic carbon and pyrite (Berner, 2005).

To the extent to which the models are validated by a range of different proxies (e.g. Berner *et al.*, 2003a; Scott and Glasspool, 2006), plant geophysical effects on atmospheric O_2 appear substantial and are controversially linked with a range of biological evolutionary radiations and events (Ward *et al.*, 2006; Falkowski *et al.*, 2005; Berner *et al.*, 2007; Labandeira, 2007). In this latter regard, plants may act as geobiological agents of terrestrial biotic evolution. Most notably, the Permo-Carboniferous rise in O_2 levels is coincident with the

appearance in the fossil record of a spectacular episode of gigantism in insects, as well as other arthropods and terrestrial vertebrates (Graham *et al.*, 1995). At this time, Carboniferous dragonfly wing-spans reached 71 cm and thorax widths 2.8 cm, and millipedes attained lengths of over 1.5 m (Graham *et al.*, 1995). The subsequent late Permian–early Triassic fall in O_2 (13–15%) saw a decrease in the level of animal gigantism, though it is worth noting that dragonflies twice as large as the largest extant forms thrived during the late Triassic and early Jurassic oxygen minimum (Okajima, 2008), an interval that also saw the appearance of high oxygen-demand groups: flying reptiles and mammals (Butterfield, 2009).

11.2.2.2 Plants, mycorrhizae, weathering and atmospheric CO_2

The geochemical carbon cycle involves the uptake of CO_2 from the atmosphere and its transformation during the weathering of continental Ca and Mg silicate minerals to dissolved bicarbonate ions in rivers that are flushed out to the oceans and precipitated as $CaCO_3$ and $MgCO_3$ minerals (Fig. 11.1) (Berner, 2004). Over tens-to-hundreds of millions of years, thermal breakdown at depth of carbonate minerals via metamorphism, diagenesis and volcanism, transfers CO_2 back to the atmosphere (Berner, 2004). Because the atmospheric carbon reservoir is several orders of magnitude smaller than that of the rock reservoir, inputs by volcanic degassing and outputs by silicate rock weathering are thought to be finely balanced, otherwise atmospheric CO_2 levels would rise or fall dramatically (Berner and Caldeira, 1997; Zeebe and Caldeira, 2008). Rates of continental silicate rock weathering are dependent upon climate (temperature and hydrology) to create a negative
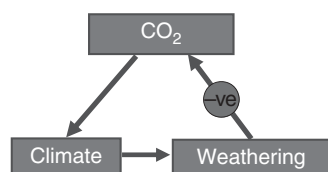
Earth's thermodynamic thermostat

Figure 11.2 Simplified systems diagram for the thermostatic control of Earth's climate via the geochemical carbon cycle. Plain arrows are positive feedbacks, those with a –ve symbol are negative feedbacks. The loop between the CO_2, climate and weathering boxes represents a negative feedback, i.e. only one –ve label. See text for further details.

feedback loop (Fig. 11.2), – that is a thermodynamic feedback control on Earth's temperature – whereby rising CO_2 causes warming and moister climates that together enhance weathering and promote CO_2 removal from the atmosphere (Walker *et al.*, 1981; Berner *et al.*, 1983c). Co-evolutionary partnerships of plants and symbiotic fungi likely accelerated mineral weathering processes removing CO_2 from the atmosphere (Berner, 1998; Berner *et al.*, 2003b; Taylor *et al.*, 2009).

The weathering of Ca silicate minerals can be simply represented by the overall reaction (Berner, 2004):

$$CO_2 + CaSiO_3 \rightarrow CaCO_3 + SiO_2 \qquad (11.3)$$
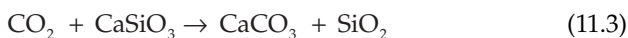
This type of reaction liberates Ca^{2+} ions that are carried to the oceans by rivers, and with dissolved bicarbonate ions, leads to the precipitation of calcium carbonate minerals. With magnesium silicates, Mg^{2+} is liberated, but exchanged with calcium in marine basalts, leading to the deposition of $CaCO_3$ rather than $MgCO_3$ (Berner, 2004). Ultimately this flux represents the net transfer of carbon from the surficial system to the rock reservoir until it is released millions of years later during metamorphism or weathering (i.e. the reverse of reaction represented by Equation 11.3). Photosynthesis by land plants, algae, and phytoplankton also transfers carbon from the ocean–atmosphere system into the lithosphere, but the masses of this organic carbon sub-cycle are smaller than those involved in the inorganic subcycle and are less important from a climatic perspective.

The advent of land plants some 470 Ma ago, and the subsequent spread of rooted trees and forests likely introduced, for the first time in Earth's history, significant biotic regulation of the global atmospheric CO_2 concentration through their collective effects on mineral weathering (e.g. Berner, 1997, 1998). The current paradigm recognizes that vascular plant activities enhance silicate mineral weathering by dissolution of bedrocks in five major ways. See Berner *et al.* (2003b) for an extensive review of the field and laboratory evidence, and Taylor *et al.* (2009) for a critical outline of the geochemical arguments:

Mechanism (i). Acidification due to hydrogen ion and organic exudates.
Mechanism (ii). Acidification due to respiration and elevated CO_2(g).
Mechanism (iii). Litter decomposition and carbon transfer to heterotrophs.
Mechanisms (iv). Recycling of evapotranspiration and repeat flushing of soils.
Mechanisms (v) Bank stabilization and retardation of soil erosion.

Mechanisms (i) to (v) above were probably strengthened by: (1) the evolution, diversification and spread of deeply rooting trees throughout upland areas from the Silurian through the Devonian (416–359 Ma ago), and (2) more contentiously, by the replacement of gymnosperms with the more advanced angiosperms from the early Cretaceous onwards (145–65 Ma ago) (Berner, 1997, 1998, 2004). Empirical representation of the effect of these two plant evolutionary axes on mineral weathering processes in long-term carbon cycle models (e.g. Berner and Kothavala, 2001, Bergman *et al.*, 2004; Berner, 1997, 1998; Volk, 1989) indicates the potential capacity of each to promote CO_2 removal from the atmosphere and alter the trajectory of Earth's CO_2 history and climate.

Current thinking about the role of plants in altering chemical weathering processes has been dominated by the prevailing view outlined above. However, this view gives only passing recognition to the possible role of fungi in weathering processes (Hoffland *et al.*, 2004; Leake *et al.*, 2008; Bonneville *et al.*, 2009; Taylor *et al.*, 2009). Yet approximately 80–90 % of plant species form symbiotic associations with mycorrhizal fungi (Read, 1991), which act as the sink for a large organic carbon flux received from plants (Högberg and Read, 2006).

A revised framework incorporating fungal and soil physiological ecology proposes that rates of biotic weathering can be more usefully conceptualized as being 'driven by, and proportional to, autotrophic carbon fixation, especially the fraction allocated belowground' (Taylor *et al.*, 2009). This suggestion is underpinned by the realization that rates of biotic weathering are 'fundamentally controlled by the energy supply to photosynthetic organisms which, in turn, controls their biomass, surface area of contact, and their capacity to interact physically and chemically with the minerals' (Taylor *et al.*, 2009). In this revised view, it is important to emphasize that it is the combined effects of vegetation, especially root activities and associated mycorrhizal fungi, that are implicated as key biotic components of weathering processes, all of which are fuelled by photosynthate fixed by the above-ground biomass.

The two major functional groups of mycorrhizal fungi have different origination dates and differ in their modes of nutrient acquisition (Taylor *et al.*, 2009). Such

differences may translate into differences in their effectiveness in driving biotic weathering processes. Arbuscular mycorrhizal fungi (AMF), exclusively of the order Glomales (Glomeromycota), are the ancestral group. Molecular clock evidence indicates they originated between 462 and 353 Ma ago (Simon *et al.*, 1993), and there is evidence in the fossil record for their association with plants by the Early Devonian (400 Ma ago) (Remy *et al.*, 1994). Ectomycorrhizal fungi (EMF) arose considerably later, probably sometime in the Jurassic, about 180 Ma ago (Berbee and Taylor, 2001). AMF penetrate cells of plant roots by forming invaginations in the cell membrane, and provide nutrients, especially phosphorus, to plants that would otherwise be inaccessible to the root systems. During growth, AMF reduce the pH of fluids around the hyphal tip both through proton release during the uptake of inorganic cations (e.g. NH_4^+) to maintain electrostatic neutrality, and by supporting AMF-associated bacteria (Villegas and Fortin, 2001, 2002). This is a crucial factor in increasing mineral dissolution and P uptake. AMF mycelial networks also secrete glycoproteinaceous compounds into the soil that increase soil particle aggregation, which could alter water cycling and cation flushing.

The plant–fungus interface of EMF is fundamentally different from that of AMF, consisting of mycelia sheaths around the absorptive root-tips of EMF-forming angiosperm and gymnosperm trees. Typically over 90% of root-tips are sheathed in mycelium so that virtually all of the labile carbon released into soils from roots is channelled through these fungi (Leake *et al.*, 2004). EMF mycelia networks extend outwards from the root-fungal mantle into the soil to mobilize and absorb nutrients by actively secreting organic acids and protons at their hyphal tips altering localized pH values and accelerating mineral dissolution (Landeweert *et al.*, 2001). AMF are not known to secrete organic acids or chelators for active mineral dissolution (Taylor *et al.*, 2009).

The proposed involvement of mycorrhizae in driving biotic weathering calls for a re-evaluation of how the rise and spread of deep-rooting trees, and the rise of angiosperms, are represented in geochemical carbon cycle models. In particular, it questions the relevance of contemporary field studies on areas of vegetation dominated by EMF-forming trees for developing empirical modelling functions describing early forest development that likely involved AMF associations (Strullu-Derrien and Strullu, 2007). Further, it also implies that falling atmospheric CO_2 levels during the Mesozoic and Cenozoic may actually be linked to the rise and spread of EMF-forming trees rather than simply being linked to the rise of angiosperms at the expense of gymnosperms. A critical appraisal of the frequently cited evidence for angiosperms being more effective at weathering than gymnosperms indicates it to be equivocal (Taylor *et al.*, 2009).

11.3 Animals as geobiological agents

Given their enormous standing biomass and domination of most terrestrial environments, it is hardly surprising that land plants serve as powerful geobiological agents. Often less appreciated is the correspondingly large impact made by animals. The key to metazoan influence lies in their underlying physiology, which in most instances combines heterotrophy and motility with organ-grade multicellularity. By tapping into an effectively inexhaustible source of novel morphology and behaviour, motile multicellular heterotrophs have revolutionized the exchange between biosphere and geosphere over the past 600 million years (Butterfield, 2007, 2011).

The essence of organ-grade animals (= eumetazoans) is the gut – a specialized multicellular chemical reactor adapted for the digestion of food, usually in collaboration with symbiotic gut microbes (Penry and Jumars, 1986). At one level, there is nothing particularly novel about this apparatus, neither the chemical nor microbial processes differing substantially from those in the external environment. However, the active maintenance of 'optimal' digestive conditions by the gut sets these phenomena in a fundamentally more efficient and purposeful context, particularly when they are integrated with other organ systems optimized for sensing, pursuing, capturing, filtering and comminuting food.

By diverting productivity away from default microbial processing to that of a roving chemical reactor, animals might be expected to increase rates of biogeochemical cycling – which in many ways they certainly do. Even so, it is worth appreciating that metazoans direct a significant proportion of digested food – generally considered to be around 10% – into a loop with fundamentally lower levels of return. Due to the three-quarter scaling relationship between body mass and metabolic rate, respiration in larger organisms is exponentially slower than in smaller ones, making animals the repositories of relatively long-lived, non-cycling biomass. In aquatic food webs, where predators tend be much larger than their prey, this size-specific metabolism extends up the trophic structure with stepwise increases in predator size balanced by correspondingly lower levels of respiration – to the extent that marine food chains exhibit broadly equivalent biomasses at each of ca. five trophic levels, from phytoplankton to sea monsters (Sheldon *et al.*, 1972; Kerr and Dickie, 2001; Brown *et al.*, 2004). With four of these five levels occupied exclusively by metazoans, it is clear the majority of marine biomass is represented by animals – the equivalent of trees on land.

Like all organisms, animals package biomass; but the stoichiometry of these packages differs substantially

from that of primary producers, varying with environment, bodysize and taxon-specific physiology (Sterner and Elser, 2002). In terrestrial ecosystems, where plants are embellished with C-rich structural macromolecules, the conversion to herbivore biomass entails a pronounced reduction in C:N/P ratios, though the effect is generally swamped by the predominance of plant biomass. In aquatic ecosystems, however, the fundamentally higher proportion of consumer biomass – an inverted trophic pyramid – means that animal stoichiometry can impinge directly on ecosystem nutrient flux (Polis, 1999).

In their review of ecological stoichiometry in lakes, Elser *et al*. (1996) compared the effects of differing types of herbivorous mesozooplankton on overall nutrient status. For zooplankton with relatively high N:P ratios such as calanoid copepods (N:P ~ 30:1), associated phytoplankton growth is typically N-limited due to the preferential retention of N in consumer biomass. By contrast, the much lower N:P of cladocerans (e.g. *Daphnia* N:P ~ 15:1) tend to induce P-limitation. The reason for such pronounced differences reflects the differing life histories of these two groups, with the very rapid growth rates and parthenogenic reproduction of *Daphnia* requiring substantially greater rates of protein synthesis and accompanying ribosomal RNA (ca. 10% of the dry weight of *Daphnia* is RNA, vs. just 2% in copepods).

The more fundamental reason for cladoceran vs. copepod domination in lacustrine systems relates to ecological tradeoffs. Thus, under severe P-limitation, Elser and colleagues found that slower growing, high N:P copepods always outcompeted cladocerans. Under more equable conditions, however, the principal control on secondary production switches from the 'bottom-up' availability of nutrients to the 'top-down' effects of predation. Unlike copepods, which are capable of inertial escape jumps, *Daphnia* are mostly constrained to viscous flow and are consequently much more susceptible to visual predation (Naganuma 1996). Thus the introduction of zooplankton-feeding minnows to *Daphnia*-dominated lakes can lead to a replacement by high N:P calenoid copepods, which in turn converts primary productivity from P-limited to N-limited conditions. Minnows, of course, are also susceptible to predation, and the introduction of higher level predators (piscivores) can induce a return to *Daphnia*-dominated zooplankton and P-limited primary production. This is a classic account of a 'trophic cascade' in which the activities of predators cascade down food chains to control both primary production and overall ecosystem function (Pace *et al*., 1999).

Trophic cascades are most strongly expressed in simple systems with strong trophic links, such as in lakes, and often fail to propagate faithfully through more complex foodwebs due to various compensatory effects (Pace *et al*., 1999). Even so, there is an increasing recognition that the top-down activities of consumers control the structure of most modern ecosystems. Recent over-fishing in the Black Sea, for example, is thought to be responsible for its increasingly frequent jellyfish blooms and rising turbidity as the removal of apex predators (bonito, mackerel, bluefish, dolphins) cascades down through zooplanktivorous fish ($\uparrow$), crustacean mesozooplankton ($\downarrow$) and phytoplankton ($\uparrow$) (Daskalov 2002). Instances of trophic cascades in open marine conditions are less easily recognized, in part because of the larger scale and more generally oligotrophic conditions, although the catastrophic and seemingly permanent shifts in population structure associated with commercial fisheries demonstrates that it does happen (e.g. Frank *et al*. 2005, Casini *et al*. 2009). A happier cascade saw the return of Pacific kelp forest communities following the 20th century recovery of sea otter populations and their top-down control on sea urchin grazing (Estes and Duggins 1995).

The fundamentally greater levels of plant biomass in terrestrial ecosystems tend to attenuate the top-down effects of consumers, though these become more apparent in simplified microcosms. In low-diversity arctic tundra, for example, the grazing activities of muskox and caribou have been shown to suppress the spread of woody shrubs (Post and Pederson 2008), and in tropical forest communities that have lost their top predators, plant biomass becomes decimated due to order-of-magnitude increases in herbivorous howler monkeys, iguanas and leaf-cutter ants (Terborgh *et al*., 2001). Such observations support the so-called 'green world' hypothesis, which holds that the terrestrial biosphere maintains its vegetated cover through the top-down control of herbivory by predators (Hairston *et al*., 1960).

There are, of course, other constraints on the activity of herbivores, not least the pronounced stoichiometric disparity between land plants and herbivores (Polis, 1999). But in terms of geobiological impact, terrestrial predators still punch well above their weight. In a temperate grassland ecosystem, for example, Schmitz (2008) demonstrated a 14% reduction in plant diversity, a 33% increase in nitrogen mineralization and a remarkable 163% increase in above ground primary productivity when spider predation on grasshoppers switched from 'sit and wait' ambush-type hunting to a more actively roaming strategy. By presenting a persistent and detectible danger, ambush hunters appear to induce a behavioural response in their prey which cascades down to affect the structure and function of the entire system.

Such pronounced, seemingly idiosyncratic amplification of individual behaviour greatly complicates the geobiological accountability of trophic interactions. One might ask, for example, what controls the presence or absence of 'sit and wait' type spiders in temperate

grasslands. Both higher-level predation and within-level competition are possibilities, but the more useful response might be to recognize the overarching effect of diversity itself (Hooper *et al.*, 2005; Duffy *et al.*, 2007). Species richness provides multiple responses to particular circumstances which can enhance productivity within a particular trophic level (Tilman *et al.*, 2001), while the presence of multiple links between trophic levels strongly attenuates the transmission of trophic cascades (McCann, 2000). But diversity is also about ecological novelty, which, under certain circumstances, can be accompanied by dramatic non-linear responses – witness any number of (un)natural experiments involving invasive species (Mooney and Cleland, 2001), from cats and cane toads to rabbits and zebra mussels.

11.3.1 Ecosystem engineering

The geobiological impact of animals extends well beyond immediate trophic effects. Like the vascular land plants discussed earlier, animals are capable of altering physical environments and thereby defining the larger-scale ecological context. The classic case of such ecosystem 'engineering' (Jones *et al.*, 1994) is the dam-building behaviour of beavers, which not only creates vast expanses of temperate wetland, but also increases habitat heterogeneity, sediment and nutrient retention, and associated biodiversity (Naiman *et al.*, 1994). A comparable degree of engineering occurs in marine settings, where coral reefs and kelp forests dissipate wave energy, stabilize sediments, and provide the framework for unique, multidimensional ecosystems (Estes and Duggins 1995, Idjadi and Edmunds, 2006; Alvarez-Filip *et al.* 2009).

Smaller animals have less individual engineering potential, but can more than make up for this through their collective activities. The addition of minnows to clear-water lakes, for example, can switch the principal zooplankton from cladocerans to slower-growing copepods, leading to increased phytoplankton densities, increased water-column turbidity, eutrophication, and bottom water anoxia. In the Lower Great Lakes (Ontario, Erie, Michigan), it was the invasion of suspension-feeding dreissenid (zebra) mussels – in concert with a multibillion dollar investment in sewage treatment – that finally restored their historical clear-water conditions (Higgins *et al.*, 2008). Ironically, the lakeshores have recently become more fouled than ever by *Cladophora glomerata* blooms, despite the fundamentally lower levels of nutrient loading. By clearing the water column of suspended phytoplankton the mussels greatly expanded the photic-zone habitat for benthic *Cladophora*, at the same time as their shell-beds created abundant new hard-substrate on which these algae can become established.

All ecosystems are engineered at some level by the organisms they support, which in turn are dependent on the nature of the ecosystem. Such interdependency gives rise to positive feedback effects and hysteresis, with ecosystems sometimes shifting dramatically between alternative stable states (Scheffer and Carpenter, 2003). Thus the cladocerans and zebra mussels responsible for clear-water conditions in lakes tend to reinforce the clear-water conditions in which they thrive, thereby increasing the system's resilience to turbidity-inducing nutrient loading. Even so, at some level of nutrient input (and/or reduced grazing) the system can be overloaded, tipping it into a stratified, turbid-water state, which is further reinforced by the exclusion of benthic suspension feeders. Under such positive feedback conditions, the original clear-water state is not recovered by simply returning to the original conditions; rather, some destabilizing overshoot is required – such as the introduction of voracious suspension-feeding mussels. But there are always other complexifying engineers: benthic feeding fish, for example, can induce significant levels of non-algal turbidity by resuspending sediment and removing macrophytes, thereby excluding benthic suspension feeders. It is this complex feedback between biologically and physically defined environment that makes the business of restoration ecology so unpredictable (Byers *et al.*, 2006).

11.3.2 Alimentation, bioturbation and biomineralization

All heterotrophic organisms are in the business of feeding which, when conducted by relatively large organisms such as animals, tends to move, mix or package aspects of the environment that would not otherwise be moved, mixed or packaged. Migratory fish, for example, transport significant amounts of marine-derived nutrients to freshwater lakes and streams (e.g. Schindler *et al.*, 2005), and the guano of sea-birds often has profound effects on the functioning of island ecosystems (Anderson and Polis, 1999).

In a similar fashion, zooplankton fertilize much of the marine shelf benthos by repackaging phytoplankton into rapidly sinking, nutrient-rich faecal pellets. Although faecal pellets are not the only means of exporting phytoplankton out of the water-column (Turner, 2002), their contribution to the 'biological pump' is both quantitatively and qualitatively significant (Wassmann, 1998, Hernández-León *et al.*, 2008). The faecal pellets and pseudo-faeces of benthic suspension-feeders also serve as an important link between the plankton and benthos, not only with respect to nutrients but by reconstituting enormous volumes of suspended clay into dense sand-sized particles (Pryor, 1978). Moreover, the osmoregulatory requirement of marine fish to continuously drink results in enormous quantities of physiologically excreted carbonate – representing as much as 15%

of total carbonate production in the modern oceans (Wilson *et al.*, 2009).

Metazoans larger than about a millimetre also introduce substantial amounts of turbulence to the environment while pursuing their individual ecologies. Although trivial in subaerial settings, it has been argued that metazoans contribute as much mechanical energy to the world's oceans as winds and tides (Huntley and Zhou, 2004, Dewar *et al.*, 2006). Whether or not such calculations are quantitatively realistic (Visser, 2007), the activities of zooplankton, fish and aquatic mammals represent a qualitatively distinct style and distribution of marine turbulence, with potentially enormous knock-on effects for marine stratification, nutrient regeneration and phytoplankton ecology.

By far the most substantial environmental mixing by animals is their bioturbation of sediments and soils. Such activity is dominated by relatively large organisms capable of moving sedimentary grains and ventilating otherwise anoxic environments (Jumars *et al.*, 1990). Like the subsurface components of vascular land plants, infaunal animals have a profound effect on substrate permeability, erodibility, carbon burial, nutrient recycling and habitat facilitation.

The geobiological consequences of animal bioturbation depend on particular infaunal behaviours. Deposit feeding, for example, results in the mixing (and/or unmixing) of constantly ingested sediment, whereas the construction of open burrow systems is likely to have greater impact on advective ventilation (Aller, 1982). Bioturbation in soils is dominated by earthworms, ants, termites and burrowing mammals, which are responsible for a wide range of engineering effects – from increased nutrient regeneration, primary productivity and carbon burial, to textural modification and aeration (e.g. Folgarait, 1998, Reichman and Seabloom, 2002, Wilkinson *et al.* 2009). By volume, it is the highly motile, non-selective deposit feeders that do the most work, while habitat heterogeneity and its compounding effects on biodiversity tend to derive from more localized 'intentional' engineers (Joquet *et al.*, 2006). Geophagous earthworms, for example, homogenize soil environments, whereas the nest-building behaviour of ants and termites gives rise to islands of concentrated influence, often in collaboration with other behaviourally complex species. Terrestrial bioturbators also play an important role in controlling landscape topography by altering soil coherence and mobility (Deitrich and Perron, 2006, Wilkinson *et al.* 2009).

Subaqueous soft sediments are fundamentally more homogeneous than soils, and are generally supplied with more digestible, nutrient-rich organic material. As such, they are intensively and (almost) ubiquitously processed by infaunal deposit and detritus feeders. Shallow water infaunal echinoids, for example,

completely rework surface sediments over the course of a few days (Lohrer *et al.*, 2004), and virtually all marine sediments are thought to pass through the guts of deposit feeders at least once before final burial (Jumars *et al.*, 1990). Bioturbating marine infauna – primarily polychaetes, bivalves, echinoids and crustaceans – are also responsible for marked increases in oxygen demand, sulfide oxidation and ammonium generation, while organic carbon burial may be enhanced by sediment mixing. At a structural level, bioturbation disrupts both the physical and microbial binding of sediments resulting in relatively 'soupy' substrates and increased bottom-water turbidity. With submarine soft-sediments covering well over half the planet – and subaerial soft-sediments covering much of the rest – bioturbating animals represent one of the planet's most influential engineering guilds.

Although burrowing and necto-benthic animals tend to disrupt sub-aqueous sediments, those that live epifaunally often contribute substantially to sediment stabilization (Reise 2002). The most obvious stabilizers are colonial/modular invertebrates with a capacity to construct, baffle and bind various types of wave-resistant reefs (e.g. corals, sponges, bryozoans, oysters). As with plants on land, animal-induced stabilization in the marine realm is usually associated with relatively large body-sizes and sessile habits, though it also occurs in certain motile forms such as sediment-climbing mussels (van Leeuwen *et al.* 2010). By engineering unique high-energy environments, reef-forming metazoans also bear directly on water turbulence, wave dissipation, and shoreline dynamics (Idjadi and Edmunds, 2006, Alverez-Filip *et al.*, 2009).

One of the principal factors contributing to modern marine environments is the enormous capacity of marine invertebrates to precipitate biominerals from seawater. In addition to their structural function in reefs, biomineralized skeletons play a defining role in many level-bottom settings. The unique hydraulic properties and accompanying taphonomic feedback of metazoan bioclasts create a range of structurally and ecologically unique sedimentary environments, including spicule mats, shell beds and cheniers (Kidwell and Jablonski, 1983, Liu and Walker, 1989, Bett and Rice, 1992, Gutierrez *et al.*, 2003).

Metazoan biomineralization also contributes significantly to ocean chemistry through the enzymatically enhanced precipitation of carbonate and silica, though it is unicellular protists – most notably coccolithophores and diatoms – that currently determine the larger-scale, biogeochemical impact of biomineralization. Even so, there is a strong case for linking the evolution of biomineralizing phytoplankton to the escalatory effects of grazing metazoan zooplankton (Smetacek, 2001; Hamm *et al.*, 2003), which would make animals responsible – either

directly or indirectly – for the majority of biomineral production in the modern ocean.

11.3.3 Evolutionary engineering and the Ediacaran–Cambrian radiations

The overarching effect of animal ecology on environment identifies the modern biosphere as fundamentally and pervasively metazoan. This was not always the case, however, and it is clear that the style and degree of influence has varied over evolutionary time (Erwin, 2008). At some point in the past beavers did not build dams, earthworms did not mix soil, and there were no coccolithophores or coral reefs. Bioturbation has been a feature of most marine sediments for the past 550 million years, but the intense 'biological bulldozing' typical of the modern oceans is a relatively recent, Mesozoic, invention (Thayer, 1983). Indeed, it was not so long ago that animals had yet to evolve, and ecosystems were engineered exclusively by microbes. Consideration of this pre-metazoan 'microbial world,' and its transition into the Phanerozoic, offers a unique view of how animals came to dominate the structure and function of the modern biosphere (Butterfield, 2007, 2009, 2011).

Whether animals – specifically organ-grade eumetazoans – have deep Proterozoic roots is a matter of long-standing debate, but it is clear that they were of no geobiological significance until the Ediacaran. Not only is there no fossil record of pre-Ediacaran eumetazoans, but the profound evolutionary stasis expressed by contemporaneous microfossils reflects the absence of any significant co-evolutionary drivers, at least with respect to organism size or morphology (Peterson and Butterfield, 2005; Butterfield, 2007). The break comes in the earliest Ediacaran, which sees an unprecedented radiation of large, morphologically complex microfossils and an order-of-magnitude increase in rates of evolutionary turnover – indirect but compelling evidence for the appearance of organ-grade eumetazoans. A further early Cambrian radiation of microfossils – this time representing phytoplankton – is most reasonably interpreted as a co-evolutionary response to the appearance of metazoan zooplankton, with myriad feedback effects driving the Cambrian explosion of large animals (Butterfield, 1997, 2007, 2011).

Interestingly, the Ediacaran and early Cambrian also represent an interval of pronounced change in oceanic chemistry and structure, including a switch from cyanobacteria- to algae-dominated export production (Knoll *et al.*, 2007), increased rates of vertical transport (Logan *et al.*, 1995), and a progressive ventilation/oxygenation of the deep ocean (Canfield *et al.*, 2007). The conventional interpretation of these data is that they reflect 'bottom-up' shifts in biogeochemical cycling, giving rise to an oxygenated atmosphere and the 'permissive environments' that allowed both eukaryotic algae and animals to pursue their full evolutionary potential. There is, however, an alternative 'top down' interpretation, which recognizes animals as powerful, context-altering, geobiological agents – the cause rather than the consequence of geochemical perturbation (e.g. Logan *et al.*, 1995; Butterfield, 1997, 2007, 2009, 2011). Qualitative shifts in the Neoproterozoic-Cambrian sulfur record, for example, have recently been ascribed to the onset of bioturbation-induced sulphide oxidation (Canfield and Farhquar 2009).

Insofar as animals play a fundamental role in structuring aquatic ecosystems, it is clear that the pre-Cambrian and pre-Ediacaran oceans must have operated in a fundamentally different manner than their modern counterparts. Certainly the absence of Phanerozoic-style biomineralization and bioturbation would have imparted a distinctly non-uniformitarian quality to early benthic environments, with important implications for sediment stability, benthic ecology and biogeochemistry (Aller, 1982, Seilacher, 1999, Droser *et al.*, 2005, Canfield and Farquhar, 2009). In the pelagic realm, the absence of metazoans would have precluded the faecal export of surface productivity (Logan *et al.*, 1995), as well as the calcium carbonate currently generated by fish (Wilson *et al.*, 2009).

But animals do more than engineer physical environments. They are also powerful agents of co-evolutionary change, directly responsible for the Phanerozoic radiations of organism size, morphology and biomineralization (Vermeij, 1994, Butterfield, 2007, 2011). Body size is of particular significance in aquatic ecology, and in the case of phytoplankton there is a clear advantage – in terms of buoyancy, nutrient scavenging and self-shading – for maintaining small cell size. The paradox in the modern oceans is that the vast majority of export production is represented by relatively large-celled, morphologically diverse, and often substantially biomineralized eukaryotic phytoplankton (Hutchinson, 1961) – for which the best explanation is a top-down ecological trade-off imposed by suspension-feeding zooplankton (Smetacek, 2001; Jiang *et al.*, 2005). In the (pre-metazoan) absence of such selective pressures, phytoplankton are expected to be both small and non-biomineralizing, leading to fundamentally lower rates of sinking, increased surface-water turbidity, and a compounding positive feedback in favour of stratified, cyanobacteria-dominated oceans – all of which are features of the Proterozoic record (Knoll *et al.*, 2007; Canfield *et al.*, 2007; Butterfield, 2009). Given the sudden, often profound regime shifts associated with ecological perturbation in modern ecosystems (Scheffer and Carpenter, 2003), the Ediacaran introduction of organ-grade metazoans can be usefully viewed as the tip-off point between two alternative stable states in planetary function

(Butterfield, 2007, 2009, 2011): on the one hand a microbial world dominated by prokaryotic ecologies and evolutionary stasis, and on the other the extraordinarily diverse and dynamic world of the Phanerozoic.

11.4 Conclusions

Multicellular plants and animals clearly have an overarching impact on ecosystem function in the Phanerozoic, and there is little doubt that the biosphere would have worked in fundamentally different way prior to their appearance. All organisms act as geobiological agents, but the influence of any one component is highly dependent on the overall context, with a potential for powerful, highly idiosyncratic and non-linear feedbacks. Certainly the evolution of land plants gave rise to conditions that encouraged the proliferation of land plants and exerted profound impacts on the Earth system (Beerling, 2007), while the rise of animals inevitably constructed the opportunities for ever more animals.

Both animals and plants engineer novel environments, but they also engineer one another over evolutionary time scales. Land plant diversity is pervasively linked to the co-evolutionary effects of animals – most obviously in the form of pollination mutualisms and top-down responses to herbivory (Fenster *et al*., 2004; Holdo *et al*., 2009) – but so, too has terrestrial animal diversity been facilitated and driven by plants. Thus the great radiations of Tertiary mammals were as much a product of evolving grasses and expanding grasslands as the expansion of grasslands was driven by the co-evolutionary radiation of mammals, disease and fire (Retallack, 2001; Holdo *et al*., 2009; Gill *et al*., 2009). More recent evolutionary and technological innovations have of course expanded the geobiological influence of plants and animals out of all proportion, reengineering planetary environments, climate and biodiversity as they pursue their own evolutionary advantage.

Acknowledgements

References

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytologist* **165**, 351–372.

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. *Plant, Cell and Environment* **30**, 258–270.

Algeo TJ, Scheckler SE (1998) Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society* **B353**, 113–130.

Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: *Animal-Sediment Relations* (eds McCall PL, Tevesz MSS). Plenum Press, New York, pp., 53–102.

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B* **276**, 3019–3025.

Anderson WB, Polis GA (1999) Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* **118**, 324–332.

Bala G, Caldeira K, Wickett M., *et al*. (2007) Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of the National Academy of Sciences* **104**, 6550–6555.

Bartdorff O, Wallmann K, Latif M, Semenov V (2008) Phanerozoic history of atmospheric methane. *Global Biogeochemical Cycles* **22**, doi:10.1029/2007GB002985.

Beerling DJ (2007) *The Emerald Planet. How Plants Changed Earth's History*. Oxford University Press, Oxford.

Beerling DJ, Berner RA (2005) Feedbacks and the coevolution of plants and atmospheric CO_2. *Proceedings of the National Academy of Sciences* **102**, 1302–1305.

Beerling DJ, Woodward FI (2001) *Vegetation and the Terrestrial Carbon Cycle. Modelling the First 400 Million Years*. Cambridge University Press, Cambridge.

Beerling DJ, Hewitt CN, Pyle JA, Raven JA (2007) Critical issues in trace gas biogeochemistry and global change. *Philosophical Transactions of the Royal Society* **A365**, 1629–1642.

Beerling DJ, Berner RA, MacKenzie FT, Harfoot MB, Pyle JA (2009) Methane and the CH_4-related greenhouse over the past 400 million years. *American Journal of Science* **309**, 97–113.

Berbee ML, Taylor JW (1993) Dating the evolutionary radiations of the true fungi. *Canadian Journal of Botany* **71**, 1114–1127.

Bergman NM, Lenton TM, Watson AJ (2004) COPSE: a new model of biogeochemical cycling over Phanerozoic time. *American Journal of Science* **304**, 397–437.

Berner RA (1997) The rise of plants and their effect on weathering and atmospheric CO_2. *Science* **276**, 544–546.

Berner RA (1998) The carbon cycle and CO_2 over Phanerozoic time: the role of land plants. *Philosophical Transactions of the Royal Society* **B353**, 75–82.

Berner RA (2005) The carbon and sulphur cycles and atmospheric oxygen from middle Permian to middle Triassic. *Geochimica et Cosmochimica Acta* **69**, 3211–3217.

Berner RA (2004) *The Phanerozoic Carbon Cycle: CO_2 and O_2*. Oxford University Press, Oxford.

Berner RA, Caldeira K (1997) The need for mass balance and feedback in the geochemical carbon cycle. *Geology* **25**, 955–956.

Berner RA, Canfield DE (1989) A new model of atmospheric oxygen over Phanerozoic time. *American Journal of Science* **289**, 333–361.

Berner RA, Kothavala Z (2001) GEOCARB III: a revised model of atmospheric CO_2 over Phanerozoic time. *American Journal of Science* **301**, 182–204.

Berner RA, Lasaga AC, Garrels RM (1983c) The carbonate-silicate geochemical cycle and its effect on atmospheric carbon dioxide over the past 100 million years. *American Journal of Science* **283**, 641–683.

Berner RA, Beerling DJ, Dudley R, Robinson JM, Wildman RA (2003a) Phanerozoic atmospheric oxygen. *Annual Reviews of Earth and Planetary Sciences* **31**, 105–134.

Berner EK, Berner RA, Moulton KL (2003b) Plants and mineral weathering: present and past. *Treatise on Geochemistry* **5**, 169–188.

Berner RA, VandenBrooks JM, Ward PD (2007) Oxygen and evolution. *Science* **316**, 557–558.

Bett BJ, Rice AL (1992) The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the Porcupine Seabight (bathyal NE Atlantic). *Ophelia* **36**, 217–226.

Betts RA, Cox PM, Lee SE, Woodward FI (1997) Contrasting physiological and structural vegetation feedbacks in climate change simulations. *Nature* **387**, 796–799.

Bonan GB (2008) Forests and climate change: forcings, feedbacks and the climate benefits of forests. *Science* **320**, 1444–1449.

Bonneville S, Smits MM, Brown A, *et al*. (2009) Plant-driven fungal weathering: early stages of mineral alteration at the nanometre scale. *Geology* **37**, 615–618.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

Buckley TN (2005) The control of stomatal water balance. *New Phytologist* **168**, 275–291.

Burd AB, Jackson GA (2009) Particle aggregation. *Annual Review of Marine Science* **1**, 65–90.

Butterfield NJ (1997) Plankton ecology and the Proterozoic–Phanerozoic transition. *Paleobiology* **23**, 247–262.

Butterfield NJ (2007) Macroecovolution and macroecology through deep time. *Palaeontology* **50**, 41–55.

Butterfield NJ (2009) Oxygen, animals and oceanic ventilation – and alternative view. *Geobiology* **7**, 1–7.

Butterfield NJ (2011) Animals and the invention of the Phanerozoic Earth system. Trends in *Ecology & Evolution*, **26**, 81–87.

Byers JE, Cuddington K, Jones C.G, *et al*. (2006) Using ecosystem engineers to restore ecological systems. *Trends in Ecology and Evolution* **21**, 493–500.

Canfield DE, Farquhar JE (2009) Animal evolution, bioturbation, and the sulfate concentration of the oceans. *Proceedings of the National Academy of Sciences*, *USA* **106**, 8123–8217.

Canfield DE, Poulton SW, Narbonne GM (2007) Late-Neoproterozoic deep ocean oxygenation and the rise of animal life. *Science* **315**, 92–95.

Casini M, Hjelm J, Molinero J.-C, *et al*. (2009) Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences*, *USA* **106**, 197–202.

Chapin FS, Sturm M, Serreze MC (2005) Role of land-surface changes in Arctic summer warming. *Science* **310**, 627–628.

Charney JG (1975) Dynamics of deserts and droughts in the Sahel. *Quarterly Journal of the Meteorological Society* **101**, 193–202.

Charney JG, Stone PH, Quirk WJ (1975) Drought in the Sahara: a biogeophysical feedback mechanism. *Science* **187**, 434–435.

Claeys M, Graham B, Vas G, *et al*. (2004) Formation of secondary organic aerosols through photooxidation of isoprene. *Science* **303**, 1173–1176.

Crowley TJ, North GR (1991) *Paleoclimatology*. Oxford University Press, Oxford.

Daskalov, G. M. (2002) Overfishing drives a trophic cascade in the Black Sea. *Marine Ecology Progress Series* **225**, 53–63.

DeConto RM, Brady EC, Bergengren J, Hay WW (2000) Late-Cretaceous climate, vegetation and ocean interactions. In: *Warm climates in Earth history* (eds Huber BT, MacLeod KG, Wing SL). Cambridge University Press, Cambridge, pp. 275–296.

Denman KL, Brasseur G, Chidthaisong A, *et al*. (2007) Couplings between changes in the climate system and biogeochemistry. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, *et al*.). Cambridge University Press, Cambridge, pp.499–587.

Dewar WK, Bingham RJ, Iverson RL, Nowacek DP, St. Laurent LC, Wiebe PH (2006) Does the marine biosphere mix the ocean? *Journal of Marine Research* **64**, 541–561.

deYoung B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L, (2004) Detecting regime shifts in the ocean: data considerations. *Progress in Oceanography* **60**, 143–164.

Dietrich WE, Perron JT (2006) The search for a topographic signature of life. *Nature* **439**, 411–418.

Droser ML, Jensen S, Gehling JG (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**, 12572–12576.

Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* **10**, 522–538.

Elser JJ, Dobberfuhl D, Mackay NA, Schampel JH (1996) Organism size, life history, and N:P stoichiometry: towards a unified view of cellular and ecosystem processes. *BioScience* **46**, 674–684.

Erwin DH (2008) Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in Ecology and Evolution* **23**, 304–310.

Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* **65**, 75–100.

Falkowski PG, Barber RT, Smetacek V (1998) Biogeochemical controls and feedbacks on ocean primary productivity. *Science* **281**, 200–206.

Falkowksi PG, Katz ME, Milligan AJ, *et al*. (2005) The rise of oxygen over the past 205 million years and the evolution of large placental mammals. *Science* **309**, 2202–2204.

Fehsenfeld F, Calvert J, Fall R, *et al*. (1992) Emissions of volatile organic compounds from vegetation and their implications for atmospheric chemistry. *Global Biogeochemical Cycles* **6**, 389–430.

Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD (2004) Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution and Systematics* **35**, 375–403.

Flückiger J, Blunier T, Stauffer B, *et al*. (2004) N_2O and CH_4 variations during the last glacial episode: insight into global

processes. *Global Biogeochemical Cycles* **18**, doi:10.1029/2003GB 002122.

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation* **7**, 1221–1244.

Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**, 1621–1623.

Galy V, France-Lanord C, Beyssac O, Faure P, Kudrass H, Palhol F (2007) Efficient carbon burial in the Bengal fan sustained by the Himalyan erosional system. *Nature* **450**, 407–410.

Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS (2009) Plant communities, and enhanced fire regimes in North America. *Science* **326**, 1100–1103.

Grace JC, Lloyd J, McIntyre J, *et al*. (1995) Fluxes of carbon dioxide and water vapour over an undisturbed tropical forest in south-west Amazonia. *Global Change Biology* **1**, 1–12.

Graham JB, Dudley R, Aguilar NM, Gans C (1995) Implications of the late Palaeozoic oxygen pulse for physiology and evolution. *Nature* **375**, 117–120.

Greb, SF, DiMichele WA, Gastaldo, RA (2006) Evolution and importance of wetlands in Earth history. *Geological Society of America Special Paper* **399**, 1–40.

Gragnani A, Scheffer M, Rinaldi S (1999) Top-down control of cyanobacteria: a theoretical analysis. *American Naturalist* **153**, 59–72.

Guenther A, Karl T, Harley P, Wiedinmyer C, Palmer PI, Geron C (2006) Estimates of global terrestrial isoprene emissions using MEGAN (Model of Emissions of Gases and Aerosols from Nature). *Atmospheric Chemistry and Physics* **6**, 107–173.

Gutiérrez JL, Jones CG, Strayer DL Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos, **101**, 79–90.

Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *American Naturalist* **94**, 421–425.

Hamm CE, Merkel R, Springer O, Jurkojc P, Maier C, Prechtel K, Smetacek V (2003) Architecture and material properties of diatom shells provide effective mechanical protection. *Nature* **421**, 841–843.

Hedges JI, Keil RG, Benner R (1997) What happens to terrestrial organic matter in the ocean? *Organic Geochemistry* **27**, 195–212.

Hernádez-León S, Fraga C, Ikeda T (2008) A global estimation of mesozooplankton ammonium excretion in the open ocean. *Journal of Plankton Research* **30**, 577–585.

Higgins SN, Malkin SY, Howell ET, *et al*. (2008) An ecological review of *Cladophora glomerata* (Chlorophyta) in the Laurentian Great Lakes. *Journal of Phycology* **44**, 839–854.

Hoffland E, Kuyper TW, Wallander H, *et al*. (2004) The role of fungi in weathering. *Frontiers in Ecology and the Environment* 2, 258–264.

Högberg P, Read DJ (2006) Towards a more plant physiological perspective on soil ecology. *Trends in Ecology and Evolution* **21**, 548–554.

Holdo RM, Sinclair ARE, Dobson AP, *et al*. (2009) A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biology* **7**, e1000210, doi:10.1371/journal.pbio.1000210.

Hooper DU, Chapin FS. III, Ewel, JJ, *et al*. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.

Huber BT, MacLeod KG, Wing SL (2000) *Warm Climates in Earth History*. Cambridge University Press, Cambridge.

Huntley ME, Zhou M (2004) Influence of animals on turbulence in the sea. *Marine Ecology Progress Series* 273, 65–79.

Hutchinson GE (1961) The paradox of the plankton. *American Naturalist* 95, 137–145.

Idjadi JA, Edmunds PJ (2006) Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. *Marine Ecology Progress Series* **319**, 117–127.

Jiang L, Schofield OME, Falkowski PG (2005) Adaptive evolution of phytoplankton cell size. *American Naturalist* **166**, 496–505.

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* **69**, 373–386.

Jouquet P, Dauber J, Lagerlöf J, Lavelle P, Lepage M (2006) Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* **32**, 153–164.

Jumars PA, Mayer LM, Deming JW, Baross JA, Wheatcroft RA (1990) Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. *Philosophical Transactions of the Royal Society of London* **A331**, 85–101.

Kerr SR, Dickie L (2001) *The Biomass Spectrum. A Predator-Prey Theory of Aquatic Production*. Columbia University Press, New York, 320pp.

Kidwell SM, Jablonski D (1983) Taphonomic feedback: Ecological consequences of shell accumulation. *In* McCall PL, Tevesz MSS (eds) Animal-sediment relations. The biogenic alteration of sediments. *Topics in Geobiology*, **2**, p. 195–248.

Kleidon A, Fraedrich K, Heimann M (2000) A green planet versus a desert world: estimating the maximum effect of vegetation on the land surface climate. *Climatic Change* **44**, 471–493.

Knoll AH, Summons RE, Waldbauer JR, Zumberge JE (2007) The geological succession of primary producers in the oceans. In: *Evolution of Primary Producers in the Sea* (eds Falkowski PG, Knoll AH). Elsevier Academic Press, Oxford, pp. 134–163.

Kump LR, Pollard D (2008) Amplification of Cretaceous warmth by biological cloud feedbacks. *Science* **320**, 195.

Labandeira C (2007) The origin of herbivory on land: initial patterns of plant tissue composition by arthropods. *Insect Science* **14**, 259–275.

Landeweert R, Hoffland E, Finlay RD, Kuyper TW, van Breemen N (2001) Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. *Trends in Ecology and Evolution* **16**, 248–254.

Leake J, Johnson D, Donnelly D, Muckle G, Boddy L, Read DJ (2004) Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. *Canadian Journal of Botany* **82**, 1016–1045.

Leake JR, Duran AL, Hardy KE, *et al*. (2008) Biological weathering in soil: the role of symbiotic root-associated fungi biosensing minerals and directing photosynthate-energy into grain-scale mineral weathering. *Minerological Magazine* **72**, 85–89.

Liu C, Walker HJ (1989) Sedimentary characteristics of cheniers and the formation of the chenier plains of east China. *Journal of Coastal Research* **5**, 353–368.

Logan GA, Hayes JM, Hieshima GB, Summons RE (1995) Terminal Proterozoic reorganization of biogeochemical cycles. *Nature* **376**, 53–56.

Lohrer AM, Thrush SF, Gibbs MM (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* **431**, 1092–1095.

McCann K (2000) The diversity-stability debate. *Nature* **405**, 228–233.

Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences, USA* **98**, 5446–5451.

Naganuma T (1996) Calanoid copepods: linking lower-higher trophic levels by linking lower-higher Reynolds numbers. *Marine Ecology Progress Series* **136**, 311–313.

Naiman RJ, Pinay G, Johnston CA, Pastor J (1994) Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* **75**, 905–921.

Okajima R (2008) The controlling factors limiting maximum body size of insects. *Lethaia* **41**, 423–430.

Otto-Bliesner BL, Upchurch GR (1997) Vegetation-induced warming of the high latitude regions during the Late Cretaceous period. *Nature* **385**, 804–807.

Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**, 483–488.

Penry DL, Jumars PA (1986) Chemical reactor analysis and optimal digestion. *BioScience* **36**, 310–315.

Peterson KJ, Butterfield NJ (2005) Origin of the Eumetazoa: testing ecological predictions of molecular clocks against the Proterozoic fossil record. *Proceedings of the National Academy of Sciences, USA* **102**, 9547–9552.

Polis GA (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* **86**, 3–15.

Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences, USA* **105**, 12353–12358.

Pryor WA (1975) Biogenic sedimentation and alteration of argillaceous sediments in shallow marine environments. *Geological Society of America Bulletin* **86**, 1244–1254.

Raven JA, Edwards D (1998) Roots: evolutionary origins and biogeochemical significance. *Journal of Experimental Botany* **52**, 381–401.

Read DJ (1991) Mycorrhizas in ecosystems. *Experimentia* **47**, 376–391.

Reichman OJ, Seabloom EW (2002) The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology and Evolution* **17**, 44–49.

Reise K (2002) Sediment mediated species interactions in coastal waters. *Journal of Sea Research*, **48**, 127–141.

Remy W, Taylor TN, Hass H, Kerp H (1994) Four hundred-million-year-old vesicular arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences, USA* **91**, 11841–11843.

Retallack GJ (2001) Cenozoic expansion of grasslands and climatic cooling. *Journal of Geology*, **109**, 407–426.

Robinson JM (1990a) Lignin, land plants, and fungi: biological evolution affecting Phanerozoic oxygen balance. *Geology* **15**, 607–610.

Robinson JM (1990b) The burial of organic carbon as affected by the evolution of land plants. *Historical Biology* **5**, 189–201.

Sellers PJ, Dickinson R, Randall D, *et al.* (1996) Comparison of radiative and physiological effects of doubled atmospheric CO_2 on climate. *Science*, **271**, 1402–1406.

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* **18**, 648–656.

Schindler DE, Leavitt PR, Brock CS, Johnson SP, Quay PD (2005) Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska *Ecology* **86**, 3225–3231.

Schmitz OJ (2008) Effects of predator hunting mode on grassland ecosystem function. *Science* **319**, 952–954.

Scott AC, Glasspool IJ (2006) The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. *Proceedings of the National Academy of Sciences, USA* **109**, 10861–10865.

Seilacher A (1999) Biomat-related lifestyles in the Precambrian. *Palaios*, **14**, 86–93.

Sharkey TD, Wiberley AE, Donohue AR (2008) Isoprene emissions from plants: why and how. *Annals of Botany* **101**, 5–18.

Sheldon RW, Prakash A, Sutcliffe WH (1972) The size distribution of particles in the ocean. *Limnology and Oceanography* **17**, 327–340.

Simon L, Bousquet J, Levesque RC, Lalonde M (1993) Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. *Nature* **363**, 67–69.

Smetacek V (2001) A watery arms race. *Nature* **411**, 745.

Spracklen DV, Bonn B, Carslaw KS (2008) Boreal forests, aerosols, and the impact on clouds and climate. *Philosophical Transactions of the Royal Society* **A366**, 4613–4626.

Sterner RW, Elser JJ (2002) *Ecological Stoichiometry, the Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, NJ.

Strack JE, Pielke RA, Liston GE (2007) Arctic tundra shrub invasion and soot deposition: consequences for spring snow melt and near-surface air temperatures. *Journal of Geophysical Research* **112**, doi: G04S44.

Strullu-Derrien C, Strullu DG (2007) Mycorrhization of fossil and living plants. *Comptes Rendus Palevol.* **6**, 483–494.

Sturm M, Douglas T, Racine C, Liston BE (2005) Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research* **110**, doi: 10.1029/2005JG000013.

Taylor LL, Leake JR, Quirk J, Hardy K, Banwart SA, Beerling DJ (2009) Biological weathering and the long-term carbon cycle: integrating mycorrhizal evolution into the current paradigm. *Geobiology* **7**, 171–191.

Terborgh J, Lopez L, Nunez V, *et al.* (2001) Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926.

Thayer CW (1983) Sediment-mediated biological disturbances and the evolution of the marine benthos. In: *Biotic Interactions in Recent and Fossil Benthic Communities* (eds Tevesz MJS, McCall PL). Plenum Press, New York, pp. 480–625.

Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001) Diversity and productivity in a long-term grassland experiment. *Science* **294**, 843–845.

Tunved P, Hansson HC, Kerminen VM, *et al*. (2006) High natural aerosol loading over boreal forests. *Science* **312**, 261–263.

Turner JT (2002) Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. *Aquatic Microbial Ecology* **27**, 57–102.

Upchurch GR, Otto-Bliesner BL, Scotese C (1998) Vegetation-atmosphere interactions and their role in global warming during the latest Cretaceous. *Philosophical Transactions of the Royal Society* **B353**, 97–112.

van Leeuwen B, Augustijn DCM, van Wesenbeeck, BK, Hulscher SJMH de Vries MB (2010) Modeling the influence of a young mussel bed on fine sediment dynamics on an intertidal flat in the Wadden Sea. *Ecological Engineering*, 36, 145–153.

Vermeij GJ (1994) The evolutionary interaction among species: selection, escalation, and coevolution. *Annual Review of Ecology and Systematics* **25**, 219–236.

Villegas J, Fortin JA (2001) Phosphorus solubilization and pH changes as a result of the interactions between soil bacteria and arbuscular mycorrhizal fungi on a medium containing NH_4 as nitrogen source. *Canadian Journal of Botany* **79**, 865–870.

Villegas J, Fortin JA (2002) Phosphorus solubilization and pH changes as a result of the interactions between soil bacteria and arbuscular mycorrhizal fungi on a medium containing NH_3^- as nitrogen source. *Canadian Journal of Botany* **80**, 571–576.

Visser AW (2007) Biomixing of the oceans? *Science* **316**, 838–839.

Volk T (1989) Rise of angiosperms as a factor in long-term climate cooling. *Geology* **17**, 107–110.

Walker JCG, Hays PB, Kasting JF (1981) A negative feedback mechanism for the long-term stabilization of earth's surface temperature. *Journal of Geophysical Research* **86**, 9776–9782.

Ward P, Labandeira C, Laurin M, Berner RA (2006) Romer's gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. *Proceedings of the National Academy of Sciences, USA* **103**, 16818–16822.

Wassmann P (1998) Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. *Hydrobiologia* **363**, 29–57.

Wellman CH, Osterloff PL, Mohiuddin U (2003) Fragments of the earliest land plants. *Nature* **425**, 282–285.

Wilkinson MT, Richards PJ, Humphreys GS (2009) Breaking ground: pedological, geological, and ecological implications of soil bioturbation. *Earth-Science Reviews* **97**, 254–269.

Wilson RW, Millero FJ, Taylor JR, *et al*. (2009) Contribution of fish to the marine inorganic carbon cycle. *Science* **323**, 359–362.

Woodward FI (2007) Global primary production. *Current Biology* **17**, R269–R273.

Zeebe RE, Caldeira K (2008) Close mass balance of long-term carbon fluxes from ice-core CO_2 and ocean chemistry records. *Nature Geoscience* **1**, 312–315.