nature geoscience

FOCUS | REVIEW ARTICLE

PUBLISHED ONLINE: 1 FEBRUARY 2012 | DOI: 10.1038/NGEO1376

Palaeozoic landscapes shaped by plant evolution

Martin R. Gibling* and Neil S. Davies†

Fluvial landscapes diversified markedly over the 250 million years between the Cambrian and Pennsylvanian periods. The diversification occurred in tandem with the evolution of vascular plants and expanding vegetation cover. In the absence of widespread vegetation, landscapes during the Cambrian and Ordovican periods were dominated by rivers with wide sand-beds and aeolian tracts. During the late Silurian and Devonian periods, the appearance of vascular plants with root systems was associated with the development of channelled sand-bed rivers, meandering rivers and muddy floodplains. The widespread expansion of trees by the Early Pennsylvanian marks the appearance of narrow fixed channels, some representing anabranching systems, and braided rivers with vegetated islands. We conclude that the development of roots stabilized the banks of rivers and streams. The subsequent appearance of woody debris led to log jams that promoted the rapid formation of new river channels. Our contention is supported by studies of modern fluvial systems and laboratory experiments. In turn, fluvial styles influenced plant evolution as new ecological settings developed along the fluvial systems. We suggest that terrestrial plant and landscape evolution allowed colonization by an increasingly diverse array of organisms.

Terrestrial landscapes are dominated by a remarkable assemblage of vascular plants, mosses and liverworts, lichen, fungi, algae and microbial mats. Vegetation cover is so pervasive that we take it for granted, and some 84% of the land surface experiences geomorphological change associated with organisms[1]. Paradoxically, studies of ancient sedimentary systems have often undervalued the role of plants in shaping fluvial systems, partly because human activity has profoundly influenced vegetation along many modern rivers with which we are familiar. The science of fluvial geomorphology, for example, was based largely on channel systems that lacked a substantial load of woody debris[2]. The fundamental interaction between vegetation and landscape through the Palaeozoic era, when land plants first colonized the Earth, is receiving increased attention. This Review draws together recent contributions from the disciplines of sedimentology, palaeontology, geomorphology, ecology, engineering and experimental science.

The Palaeozoic 'greening' of terrestrial landscapes heralded a fundamental and irreversible change in sedimentation patterns, one of the most remarkable in the planet's history, and resulted in far-reaching modifications to the atmosphere, oceans and biological ecosystems (Fig. 1). These changes were set against the background of continental collision and the progressive assembly of the Pangaean supercontinent with its Himalayan-scale mountain ranges.

Biogeomorphology and the Devonian plant hypothesis

The expanding discipline of biogeomorphology owes its origin to Charles Darwin's far-sighted treatise on earthworms published late in his life, which highlighted the importance of these animals in promoting landscape denudation over geological timescales[3]. The discipline emphasizes the two-way coupling between organisms and landscapes: organisms serve as geomorphic engineers to shape landscapes to their own advantage or as an indirect consequence of their activity, and landscapes in turn influence organic evolution[1,4–8]. On a global scale, such geomorphic engineering may reflect the activity of many taxonomic groups over tens to hundreds of millions of years.

How did the Palaeozoic evolution of plants influence terrestrial landscapes? The 'Devonian plant hypothesis'[9,10] draws on known events in plant evolution, the marine record and the evolution of the atmosphere[11], inferring that the spread of vascular plants greatly influenced the Earth system because plants mediate weathering intensity through their effect on soils. As increased plant cover and root penetration enhanced bedrock weathering, nutrient runoff promoted plankton blooms in shallow seas and the extinction of goniatites and other marine fauna. Marine and coastal strata stored large amounts of carbon[12] and, as photosynthetic activity increased, the rise of atmospheric O_2 and extraction of CO_2 (Fig. 1) plunged the Earth into a major ice age by the Late Devonian. However, until recently, research on the global influence of Palaeozoic vegetation has provided little information about the terrestrial landscapes where land plants grew.

Fluvial style and plant evolution throughout the Palaeozoic

Before vegetation cover, rivers were broad bed-load systems with unstable banks[13,14]. This inference is borne out by observations of Precambrian and earliest Palaeozoic fluvial-channel deposits that demonstrate a 'sheet-braided' style (Figs 1, 2a, 3) generated by wide, shallow channels with low relief margins, and with little evidence of muddy floodplains[15–18]. Aeolian deposits were widespread, and fine sediment was largely deflated and blown out to sea[19–22]. At basin margins, some Cambro–Ordovician alluvial-fan deposits show little sand and mud, suggesting that adjoining uplands were only slightly weathered in the absence of vascular-plant cover[23]. However, by the late Proterozoic eon, increased formation of pedogenic clay minerals implies enhanced biotic soil activity and the inception of the 'clay mineral factory'[24].

Embryophytes (land plants) first appeared by the Middle Ordovician period, on the basis of discoveries of palynomorphs and plant fragments[25–28] (Fig. 1). Mud then became prominent in alluvial settings from basin-margin alluvial fans down to the coastal zone, signifying enhanced upland mud production, reduced deflation and the rise of floodplains[14]. The universal sheet-braided style gave way progressively to a 'channelled-braided' style (Fig. 3) of thick sandstone sheets composed of amalgamated lenses, suggesting that channel sediments were more cohesive and channel forms more readily preserved[18].

Through the Late Silurian and Early Devonian, many fundamental evolutionary traits appeared in plants for the first time[29], and vascular plants with water-transmission and supporting structures became abundant, although rooting structures were modest[30,31] (Fig. 2b). The enigmatic *Prototaxites* appeared, interpreted

Department of Earth Sciences, Dalhousie University, PO Box 15000, Halifax, Nova Scotia, Canada B3H 4R2. †Present address: Department of Geology and Soil Sciences, Krijgslaan 281, S8, University of Ghent, 9000 Ghent, Belgium. *e-mail: mgibling@dal.ca

NATURE GEOSCIENCE DOI: 10.1038/NGEO1376

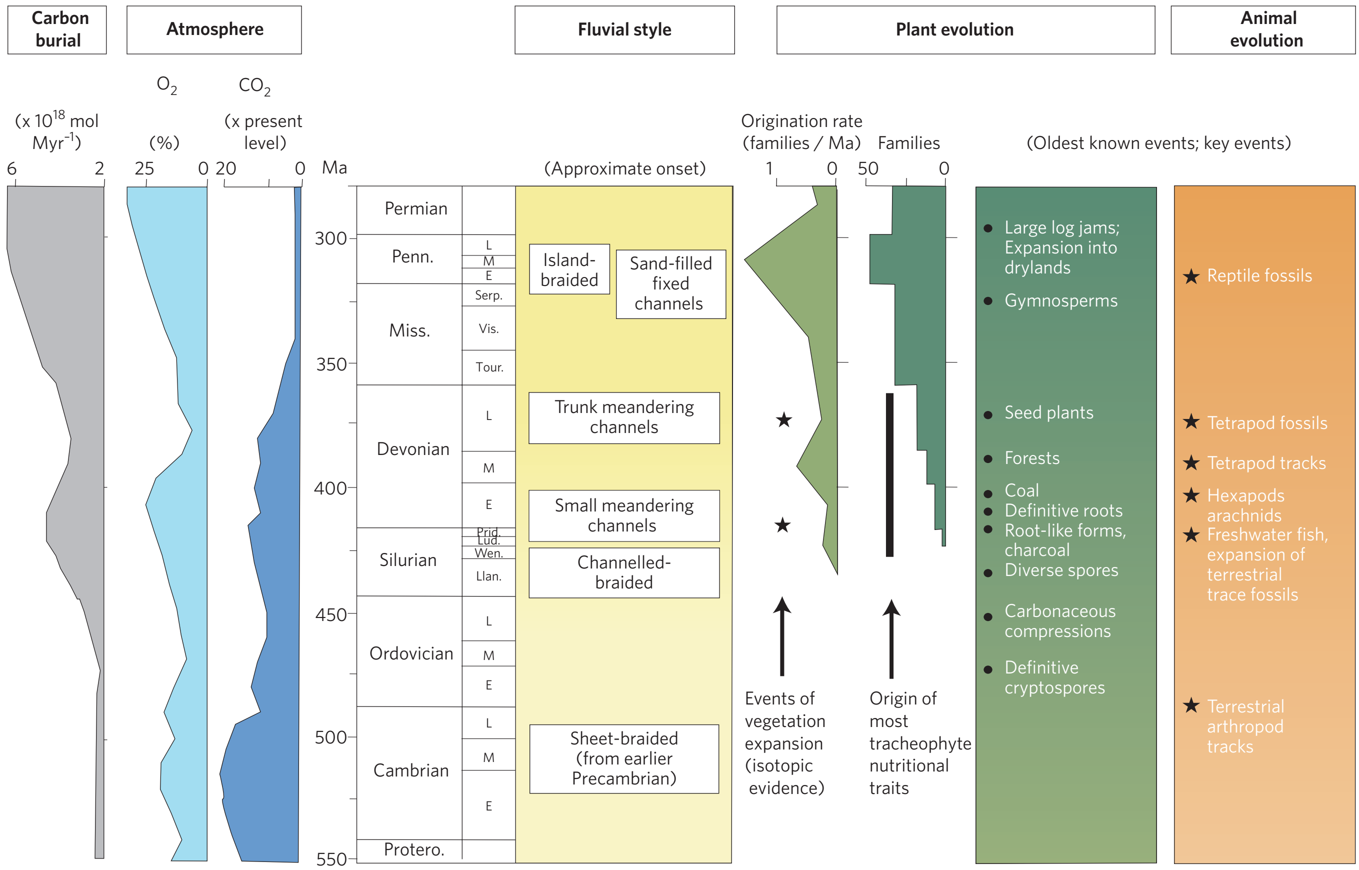

Figure 1 | Palaeozoic events of fluvial and landscape development, in relation to plant evolution and atmospheric change. Data sources: atmospheric CO_2 and O_2 curves[11], employing volcanic weathering factor in CO_2 curve, and carbon burial curve[12] (curves have wide error bars); fluvial styles and vascular-plant events[14,18,37,55]; numbers of plant families in time intervals and their origination rates[96,97]; plant nutritional traits[29]; events of rapid vegetation expansion, inferred from isotopic excursions at the Siluro–Devonian boundary[34] and at the Famennian–Frasnian boundary (Late Devonian)[41]; key events in animal evolution[88,90,93,94,98,99]; geological timescale[100]. Protero., Proterozoic; Miss., Mississippian; Penn., Pennsylvanian; Serp., Serpukhovian; Vis., Visean; Tour., Tournaisian; Prid., Pridolian; Lud., Ludfordian; Wen., Wenlockian; Llan., Llandovery.

as a gigantic fungus[32,33]. Isotopic excursions documented in marine carbonates (Fig. 1) are consistent with greatly increased vegetation cover at the Siluro–Devonian boundary[34]. By the Early Devonian, the presence of charcoal testifies to the earliest forest fires[35], the first wood appeared[36], and vegetation was sufficiently abundant to accumulate locally as peat[14].

By the latest Silurian, single-thread meandering systems appeared, identified by the presence of lateral-accretion (point bar) surfaces[37]. Initially restricted to small creeks, meandering systems are present in more than 30% of fluvial rock units of Late Devonian age, forming trunk channels (Fig. 3). Their presence signifies a considerable increase in avulsive behaviour through chute and neck cutoff and the relocation of entire channel belts. The parallel evolution of meandering rivers and rooted vegetation provides circumstantial evidence that vegetation stabilized banks and promoted systematic channel migration. In Early Devonian strata, plant fragments are found in braided-river and alluvial-fan deposits, supporting the isotopic evidence for increased plant cover[38].

By the Middle to Late Devonian, lowlands were colonized by archaeopteridalean and cladoxylalean trees, some up to 25 m tall with large roots, which formed the Earth's first dense, shady forests[39,40]. Isotopic excursions suggest that vegetation cover may have increased from 10% to 30% at the Middle–Upper Devonian boundary[41]. The Late Devonian advent of the seed habit allowed trees to colonize drier alluvial plains[42]. Mississippian plants also greatly diversified (Fig. 1), with some developing tolerance of seasonal growth and water stress (as indicated by tree rings)[43]. Late in the Mississippian, conifer pollen appeared for the first time, and the related group of cordaitalean trees, some nearly 50 m tall, became prominent[44,45]. These gymnosperms diversified early in the Pennsylvanian (Fig. 1), colonizing dry alluvial plains and even evaporitic sabkhas[46,47]. By the Pennsylvanian, vegetation was capable of growing within channels[48].

Although the prolific coal-swamp flora (Fig. 2c) is often featured as the archetypal Pennsylvanian vegetation in museum dioramas, the gymnosperm floras of alluvial plains were arguably the dominant biome, and their rise probably marked a threshold in landscape evolution. Modern conifers have a high tracheid content, which provides effective support and water transport, explaining in part their drought resistance and successful colonization of drier terrain[49]. Many modern conifers and other plants have roots that reach depths of tens of metres, allowing direct and efficient access to the water table[50]. Although Palaeozoic roots are incompletely preserved, some reached at least 4 m below the surface of well-drained alluvial plains[45]. Log jams are prominent in some Early Pennsylvanian fluvial deposits[51,52], highlighting the increased abundance of large woody debris as riparian trees grew higher and became more common, causing channel blockage and promoting break-out (avulsion). By the Mississippian, more frequent occurrences of charcoal-bearing strata indicate the importance of

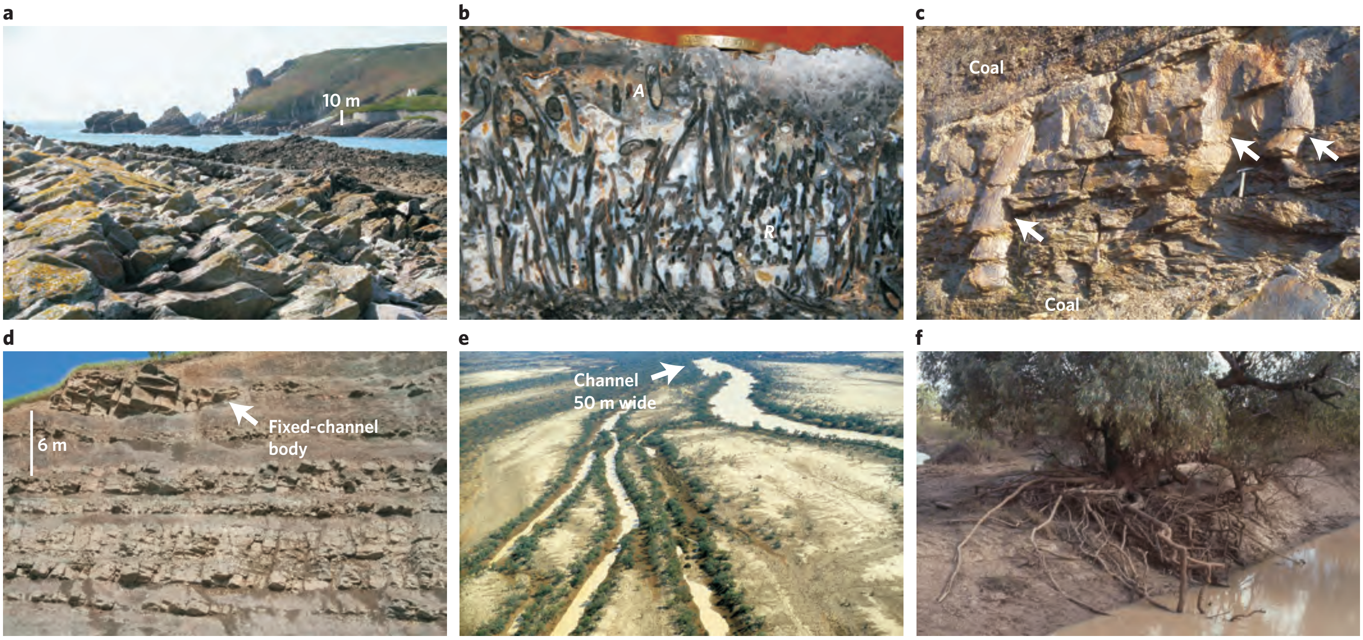

Figure 2 | Plants and fluvial systems in ancient and modern settings. a, Braided-fluvial sheets, Alderney Sandstone, Cambrian, Channel Islands. **b**, *Rhynia* (R) and *Aglaophyton* (A) in growth position in hotspring silica, Rhynie Chert, Pragian, Scotland. Pound coin is 2.3 cm in diameter (See Fig. 6a,b of ref. 31 for more detail). Image courtesy of N. Trewin. **c**, Lycopsid trees, arrowed, rooted in former peat (coal seam), Sydney Mines Formation, Middle Pennsylvanian, Canada. Hammer (centre, right) is 30 cm long. **d**, Fixed-channel body of sandstone and mudstone, possibly deposited by an anastomosing river, with red mudstone and crevasse-splay sandstone, Joggins Formation, Canada. **e**, Anastomosing Diamantina River, Queensland, Australia, with eucalyptus trees (*Eucalyptus microtheca*) along riparian zones. **f**, Extensive eucalyptus roots exposed by bank erosion, Thomson River, Queensland, Australia.

wildfire as a geomorphic agent, with strong effects on landscape stability and sedimentation[53].

Two distinctive fluvial styles appear prominently in the Pennsylvanian for the first time (Fig. 3). First, suites of channel sandstones encased in floodplain mudstones are sufficiently narrow for one or both margins to be visible in outcrop (Fig. 2d). These sand-filled fixed channels have commonly been attributed to anastomosing or anabranching rivers with several coexisting threads, although they may also represent single-thread channels that avulsed frequently. Although some mud-filled channels in Siluro–Devonian rocks may have been part of anabranching networks[54], sand-filled narrow channels first appear commonly early in the Pennsylvanian[55]. Second, within braided-river deposits, the abundance of logs filling deep channels[52] suggests comparison to modern island-braided systems that have discrete channels with abundant woody debris between vegetated islands[56]. These two fluvial styles imply the further expansion of riparian corridors and avulsive strategies (Fig. 3). They correspond broadly with the Mississippian and Pennsylvanian diversification of plants, the incoming of conifers, the expansion of vegetation across dry alluvial plains, and the appearance of large log jams (Fig. 1). More directly, the abundance of sedimentary features formed around upright trees and the preservation of upright trees on channel banks[55,57] suggest that vegetation influenced erosion and deposition on the scale of bedforms and channel belts. Although difficult to assess, vegetation had probably spread to upland bedrock tracts, or at least to upland valleys[44,52,58].

The study of molecular clocks has yielded evidence that many key evolutionary traits originated long before their first appearance in the fossil record. Although the earliest undisputed embryophyte fossils are Ordovician, embryophytes may have originated in the Precambrian, perhaps more than one billion years ago[59]. However, the influence of plants on landscape evolution is closely tied to the extent and density of vegetation, which should lag well behind the first appearances of taxa[14]. As noted above, the general accord between changes in fluvial style and macrofossil abundance suggests that the latter is a reasonable proxy for 'critical mass' in landscape evolution.

The impact of vegetation on modern landscapes

The profound influence of vegetation (largely angiosperm-dominated) on fluvial style is supported by a wealth of evidence from modern landscapes. In Australian anabranching rivers (Fig. 2e), vegetation exerts an influence on all scales from scours and vegetation shadows associated with individual trees to the sculpturing of whole channel systems[60–62]. These studies show that vegetation promotes channel stability by increasing bank cohesion and reducing erosion, principally through the binding power of roots that commonly extend below bank base or form surface mats. During dry periods, trees that become established within the channels buttress the banks and generate bars and ridges that separate the anabranches. Studies elsewhere confirm the influence of vegetation in a wide range of fluvial settings[63,64].

On the basis of field and laboratory engineering studies, the effect of root strength in stabilizing landscapes has been progressively quantified[65–68]. The root systems of individual plants are impressive (Fig. 2f), and roots play a vital role in soil and slope stability because they impart tensile strength. In some cases, roots provide virtually all the cohesive strength of the soil, with which they are frictionally coupled.

Within many channels, large woody debris accumulates in sufficient quantity to create log jams and promote channel avulsion[63,69–70], and woody debris has been cited as a crucial driver of landscape evolution[71]. In sandy braided settings, woody debris promotes bar development and island formation, especially through the regrowth of transported live wood and the germination of seeds stranded along banks during floods[56,72]. Some buried logs resist decay for thousands of years and may be reworked into modern streams, contributing to blockage[73].

NATURE GEOSCIENCE DOI: 10.1038/NGEO1376

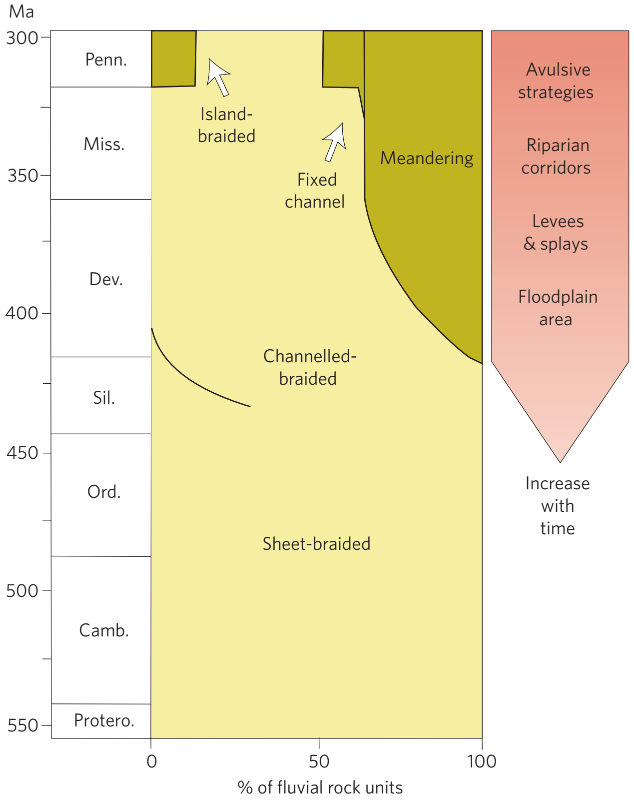

Figure 3 | Palaeozoic diversification of fluvial style. Proportions of rock units with braided, meandering and fixed-channel styles based on assessment of 330 rock units[14,55]. Meandering rivers were identified by heterolithic lateral-accretion sets, and fixed channels by ribbons to narrow sheets with vertically aggraded fill. The proportion of channelled-braided and island-braided styles is estimated, as few literature descriptions provide sufficient detail for assessment. Penn., Pennsylvanian; Miss., Mississipian; Dev., Devonian; Sil., Silurian; Ord., Ordovician; Camb., Cambrian; Protero.; Proterozoic.

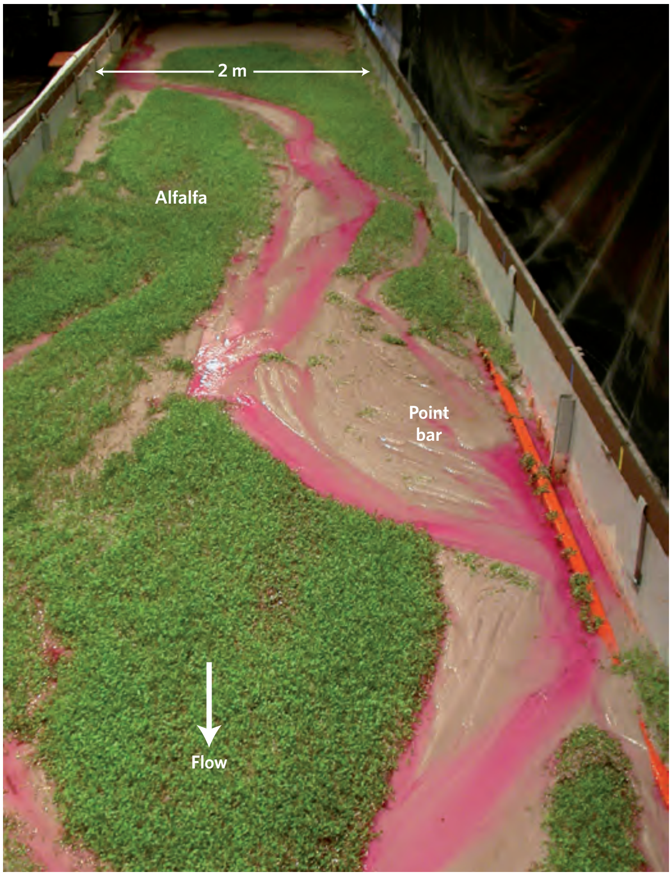

Figure 4 | Experimental study of effects of vegetation on channels. Meandering channel created in flume at St Anthony Falls Laboratory, Minneapolis. Following initial set-up of a braided channel, seeding with alfalfa (green) during low-discharge periods stabilized the banks and resulted in restriction of flow to a self-maintaining single-thread channel, shown with red dye. The channel migrated systematically, and was bordered by a stable floodplain[80]. A flume length of 10 m is shown, viewed during low flow. Image courtesy of M. Tal.

Unfortunately, we know little about alluvial tracts that have escaped human interference, and we have probably underestimated the influence of vegetation on unmodified river systems. Comparison of a pristine Australian watershed with a neighbouring one affected by agricultural activity, logging and the removal of woody 'snags' from the channels yielded arresting results[74]. The pristine channel was a narrow, winding creek, beset by fallen trees, whereas the modified channel was a straight, wide system with caving banks and rapid sediment transport. It is clear that few modern rivers are suitable analogues for Late Palaeozoic rivers. In northwest Europe, floodplain deforestation was underway by about 6,000 BP and many lowland rivers may have been anabranching before human modification[75,76].

Fluvial analogue and numerical modelling has recently made great strides in adding vegetation to the models[77–81]. Although braided rivers are only part of the planform range, earlier flume studies created virtually nothing else, suggesting that a key experimental parameter was missing. Recent experiments have modified experimental sediment surfaces by seeding them with rapidly germinating alfalfa, demonstrating that an important missing ingredient was vegetation, which suppresses the basic instability that causes braiding[78]. In all the experimental set-ups with vegetation, bank mobility and the number of active channels were reduced, leading to lower migration rates, narrower and deeper channels, and a decreased width/depth ratio. Even with a relatively sparse alfalfa cover, flows began to split around stable islands, generating an island-braided style[77,79]. By seeding alfalfa during simulated low-flow stages, researchers generated a meandering channel that, for the first time in experiments, migrated and maintained its form by balancing erosion and deposition, resulting in alluvial tracts with stable floodplains[80] (Fig. 4). Furthermore, when fine sediment is deposited in chute channels of vegetated systems, the chutes do not develop into full-scale cutoffs; this prevents the channel belts from being destroyed too rapidly and maintains a meandering style[81]. Thus, the experiments illustrate how vegetation and clay deposition promote island-braided and single-thread channels, and shift the braided planform towards an anabranching pattern[79].

Experiments have also shown that flood disturbance selectively uproots seedlings with particular root and stem characteristics, until the remaining plants are sufficiently robust to survive later floods as they are out of scale with flows that might uproot them[82,83]. These experiments highlight the ability of roots to grow sufficiently rapidly to survive uprooting during intermittent floods, and confirm the dynamic interaction between hydrology and vegetation growth over a range of timescales.

Evolving landscapes and biological evolution

Shaped themselves by plants, how may evolving landscapes have in turn influenced organic evolution? From the Silurian onwards, plant colonization ushered in a fundamental global coupling between geomorphic and biological processes, with particular importance for faunal diversification associated with standing vegetation and leaf litter[84]. New ecosystems appeared during this interval in a series of major palaeoecological events[85].

We identify three key changes in Palaeozoic fluvial systems (Fig. 3), forced by plant evolution, that would have led to positive feedbacks for both plant and animal evolution[14,55]. First, as a consequence of enhanced upland weathering, a general increase in mud from the Middle Ordovician onward produced varied lowland substrates and more accessible nutrients. Second, the development of meandering rivers with strengthened banks through the Late Silurian and Devonian promoted stable muddy floodplains partially protected by levees and highly suitable for vegetation growth and soil development, including carbonate-rich soils[14,86]. Third, Early Pennsylvanian suites of narrow fixed channels on muddy plains and of island-braided styles in sand-bed rivers imply an increased length of channel margins and riparian corridors with their varied plant communities and subsurface water prisms, which are of crucial importance for many animal species[87]. The Devonian to Pennsylvanian development of avulsive channel systems generated abandoned channels suitable for organic occupation, especially during dry periods. Towards the sea, concomitant expansion of muddy coastal plains and deltas would have also had many biological consequences. Feedback loops are likely to have been complex.

It is probably no coincidence that many key plant developments[29] took place within this diversifying alluvial framework, and these changes must collectively have influenced the evolution of animals. Although animals made intermittent passage across subaerial substrates during the Cambro–Ordovician[88], uncontroversial fossil evidence for robust terrestrial faunas is absent until the Siluro–Devonian, when vegetated muddy floodplains and plant litter became available[89]. Trace-fossil suites testify to a significant Silurian to Pennsylvanian invasion of continental ecospace, with distinctive assemblages recorded in active and abandoned channels, desiccated overbank areas and poorly drained swamps, lakes and soils[90,91]. This invasion may be linked to plant diversification, as postulated for the diversification of brackish traces[85] within evolving coastal and deltaic landscapes. Trophically modern ecosystems appeared during the Late Silurian to Middle Devonian when arthropods were feeding on sporangia, stems and fungal thalli; by the late Mississippian to Pennsylvanian, they were also targeting roots, leaves, woods and seeds[92]. For vertebrates, fish began to move into terrestrial settings during the Middle to Late Silurian[93], and there is an expanding Devonian tetrapod record with tracks known from the early Middle Devonian[94], although the earliest herbivorous tetrapods date to the Pennsylvanian[95].

The body of research reviewed here records not only the Palaeozoic invasion of the land by plants and animals over a period of some 250 million years, but also an intricate interplay between organisms and physical environments, represented in the growing discipline of biogeomorphology. Plants in particular acted as geomorphic engineers, but the diversified fluvial realm that they engineered in turn altered the framework for organic evolution.

References

1. Corenblit, D. *et al.* Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: A review of foundation concepts and current understandings. *Earth Sci. Rev.* **106,** 307–331(2011).
2. Montgomery, D. R. & Piégay, H. Wood in rivers: interactions with channel morphology and processes. *Geomorphology* **51,** 1–5 (2003).
3. Darwin, C. *The Formation of Vegetated Mould through the Action of Worms with Observation of their Habitats* (John Murray, 1883).
4. Corenblit, D., Steiger, J., Gurnell, A. M. & Tabacchi, E. Darwinian origin of landforms. *Earth Surf. Proc. Land.* **32,** 2070–2073 (2007).
5. Fisher, S. G., Heffernan, J. B., Sponseller, R. A. & Welter, J. R. Functional ecomorphology: Feedbacks between form and function in fluvial landscape ecosystems. *Geomorphology* **89,** 84–96 (2007).
6. Murray, A. B., Knaapen, M. A. F., Tal, M. & Kirwan, M. L. Biomorphodynamics: Physical-biological feedbacks that shape landscapes. *Water Resour. Res.* **44,** W11301 (2008).
7. Osterkamp, W. R., Hupp, C. R. & Stoffel, M. The interactions between vegetation and erosion: new directions for research at the interface of ecology and geomorphology. *Earth Surf. Proc. Land.* http://dx.doi.org/101002/esp.2173 (2011).
8. Jones, C. G., Lawton, J. H. & Shachak, M. Organisms as ecosystem engineers. *Oikos* **69,** 373–386 (1994).
9. Algeo, T. J., Berner, R. A., Maynard, J. B. & Scheckler, S. E. Late Devonian oceanic anoxic events and biotic crises: "Rooted" in the evolution of vascular land plants? *GSA Today* **5,** 64–66 (1995).
10. Algeo, T. J. & Scheckler, S. E. Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philos. Trans. R. Soc. Lond. B* **353,** 113–130 (1998).
11. Berner, R. A. GEOCARBSULF: A combined model for Phanerozoic atmospheric O_2 and CO_2. *Geochim. Cosmochim. Acta* **70,** 5653–5664 (2006).
12. Berner, R. A. The long-term carbon cycle, fossil fuels and atmospheric composition. *Nature* **426,** 323–326 (2003).
13. Schumm, S. A. Speculations concerning paleohydrologic controls of terrestrial sedimentation. *Geol. Soc. Am. Bull.* **79,** 1573–1588 (1968).
14. Davies, N. S. & Gibling, M. R. Cambrian to Devonian evolution of alluvial systems: The sedimentological impact of the earliest land plants. *Earth Sci. Rev.* **98,** 171–200 (2010).
15. Cotter, E. in *Fluvial Sedimentology* (ed. Miall, A. D.) 361–383 (Canadian Society of Petroleum Geologists Memoir 5, 1978).
16. Long, D. G. F. in *The Precambrian Earth: Tempos and Events* (eds Eriksson, P. G., Altermann, W., Nelson, D. R., Mueller, W. U. & Catuneanu, O.) 660–663 (Elsevier, 2004).
17. Long, D. G. F. in *From River to Rock Record: The Preservation of Fluvial Sediments and their subsequent Interpretation* (eds Davidson, S., Leleu, S. & North, C. P.) 37–61 (SEPM, 2011).
18. Davies, N. S., Gibling, M. R. & Rygel, M. C. Alluvial facies evolution during the Palaeozoic greening of the continents: case studies, conceptual models and modern analogues. *Sedimentology* **58,** 220–258 (2011).
19. Dott, R. H. Jr & Byers, C. W. SEPM research conference on modern shelf and ancient cratonic sedimentation - the orthoquartzite-carbonate suite revisited. *J. Sedim. Petrol.* **51,** 329–347 (1981).
20. Dott, R. H. Jr, Byers, C. W., Fielder, G. W., Stenzel, S. R. & Winfree, K. E. Aeolian to marine transition in Cambro-Ordovician cratonic sheet sandstones of the northern Mississippi valley, U. S. A. *Sedimentology* **33,** 345–367 (1986).
21. Dott, R. H. Jr The importance of eolian abrasion in supermature quartz sandstones and the paradox of weathering on vegetation-free landscapes. *J. Geol.* **111,** 387–405 (2003).
22. Dalrymple, R. W., Narbonne, G. M. & Smith, L. Eolian action and the distribution of Cambrian shales in North America. *Geology* **13,** 607–610 (1985).
23. Went, D. J. Pre-vegetation alluvial fan facies and processes: an example from the Cambro-Ordovician Rozel Conglomerate Formation, Jersey, Channel Islands. *Sedimentology* **52,** 693–713 (2005).
24. Kennedy, M., Droser, M., Mayer, L. M., Pevear, D. & Mrofka, D. Late Precambrian oxygenation; inception of the clay mineral factory. *Science* **311,** 1446–1449 (2006).
25. Taylor, W. A. & Strother, P. K. Ultrastructure of some Cambrian palynomorphs from the Bright Angel Shale, Arizona, USA. *Rev. Palaeobot. Palyno.* **151,** 41–50 (2008).
26. Steemans, P. *et al.* Origin and radiation of the earliest vascular land plants. *Science* **324,** 353 (2009).
27. Tomescu, A. M. F., Pratt, L. M., Rothwell, G. W., Strother, P. K. & Nadon, G. C. Carbon isotopes support the presence of extensive land floras pre-dating the origin of vascular plants. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **283,** 46–59 (2009).
28. Rubinstein, C. V., Gerrienne, P., de la Puente, G. S. l., Astini, R. A. & Steemans, P. Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). *New Phytol.* **188,** 365–369 (2010).
29. Raven, J. A. & Andrews, M. Evolution of tree nutrition. *Tree Physiol.* **30,** 1050–1071 (2010).
30. Kidston, R. & Lang, W. H. On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part I. Rhynia gwynne-vaughani, Kidston and Lang. *Trans. R. Soc. Edin.* **51,** 761–784 (1917).
31. Trewin, N. H., Fayers, S. R. & Kelman, R. Subaqueous silicification of the contents of small ponds in an Early Devonian hot-spring complex, Rhynie, Scotland. *Can. J. Earth Sci.* **40,** 1697–1712 (2003).
32. Dawson, J. W. On the fossil plants from the Devonian rocks of Canada. *Q. J. Geol. Soc. Lond.* **15,** 477–488 (1859).

33. Boyce, C. K. *et al.* Devonian landscape heterogeneity recorded by a giant fungus. *Geology* **35,** *399–402 (2007).*
34. Małkowski, K. & Racki, G. A global biogeochemical perturbation across the Silurian-Devonian boundary: Ocean-continent-biosphere feedbacks. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **276,** 244–254 (2009).
35. Glasspool, I. J., Edwards, D. & Axe, L. Charcoal in the Early Devonian: A wildfire-derived Konservat-Lagerstatte. *Rev. Palaeobot. Palyno.* **142,** 131–136 (2006).
36. Gerrienne, P. *et al.* A simple type of wood in two Early Devonian plants. *Science* **333,** 837 (2011).
37. Davies, N. S. & Gibling, M. R. Paleozoic vegetation and the Siluro-Devonian rise of fluvial lateral accretion sets. *Geology* **38,** 51–54 (2010).
38. Kennedy, K. & Gibling, M. R. The Campbellton Formation of New Brunswick, Canada: paleoenvironments in an important Early Devonian terrestrial locality. *Can. J. Earth Sci.* **48, 48,** 1561–1580 (2011).
39. Stein, W. E., Mannolini, F., Hernick, L. V., Landing, E. & Berry, C. M. Giant cladoxylopsid trees resolve the enigma of the Earth's earliest forest stumps at Gilboa. *Nature* **446,** 904–907 (2007).
40. Mintz, J. S., Driese, S. G. & White, J. D. Environmental and ecological variability of Middle Devonian (Givetian) forests in Appalachian Basin paleosols, New York, United States. *Palaios* **25,** 85–96 (2010).
41. Godderis, Y. & Joachimski, M. M. Global change in the Late Devonian: modelling the Frasnian-Famennian short-term carbon isotope excursions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **202,** 309–329 (2004).
42. Decombeix, A.-L., Meyer-Berthaud, B. & Galtier, J. Transitional changes in arborescent lignophytes at the Devonian - Carboniferous boundary. *J. Geol. Soc. Lond.* **168,** 547–557 (2011).
43. Falcon-Lang, H. J. & Galtier, J. Anatomically-preserved tree-trunks in late Mississippian (Serpukhovian, late Pendleian-Arnsbergian) braided fluvial channel facies, near Searston, southwest Newfoundland, Canada. *Rev. Palaeobot. Palynol.* **160,** 154–162 (2010).
44. Falcon-Lang, H. J. & Bashforth, A. R. Morphology, anatomy, and upland ecology of large cordaitalean trees from the Middle Pennsylvanian of Newfoundland. *Rev. Palaeobot. Palynol.* **135,** 223–243 (2005).
45. DiMichele, W. A., Cecil, C. B., Montañez, I. P. & Falcon-Lang, H. J. Cyclic changes in Pennsylvanian paleoclimate and effects on floristic dynamics in tropical Pangaea. *Int. J. Coal Geol.* **83,** 329–344 (2010).
46. Falcon-Lang, H. J. *et al.* Incised channel fills containing conifers indicate that seasonally dry vegetation dominated Pennsylvanian tropical lowlands. *Geology* **37,** 923–926 (2009).
47. Falcon-Lang, H. J. *et al.* Pennsylvanian coniferopsid forests in sabkha facies reveal the nature of seasonal tropical biome. *Geology* **39,** 371–374 (2011).
48. Fielding, C. R., Allen, J. P., Alexander, J. & Gibling, M. R. A facies model for fluvial systems in the seasonal tropics and subtropics. *Geology* **37,** 623–626 (2009).
49. Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D. & McCulloh, K. A. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **126,** 457–461 (2001).
50. Canadell, J. *et al.* Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108,** 583–595 (1996).
51. Gastaldo, R. A. & Degges, C. W. Sedimentology and paleontology of a Carboniferous log jam. *Int. J. Coal Geol.* **69,** 103–118 (2007).
52. Gibling, M. R., Bashforth, A. R., Falcon-Lang, H. J., Allen, J. P. & Fielding, C. R. Log jams and flood sediment buildup caused channel abandonment and avulsion in the Pennsylvanian of Atlantic Canada. *J. Sedim. Res* **80,** 268–287 (2010).
53. Nichols, G. J. & Jones, T. P. Fusain in Carboniferous shallow marine sediments, Donegal, Ireland: the sedimentological effects of wildfire. *Sedimentology* **39,** 487–502 (1992).
54. Marriott, S. B., Wright, V. P. & Williams, B. P. J. in *Fluvial Sedimentology VII* (eds Blum, M. D., Marriott, S. B. & Leclair, S. F.) 517–529 (Blackwell, 2005).
55. Davies, N. S. & Gibling, M. R. Evolution of fixed-channel alluvial plains in response to Carboniferous vegetation. *Nature Geosci.* **4,** 629–633 (2011).
56. Gurnell, A. M. *et al.* Wood storage within the active zone of a large European gravel-bed river. *Geomorphology* **34,** 55–72 (2000).
57. Rygel, M. C., Gibling, M. R. & Calder, J. H. Vegetation-induced sedimentary structures from fossil forests in the Pennsylvanian Joggins Formation, Nova Scotia. *Sedimentology* **51,** 531–552 (2004).
58. Bashforth, A. R., Drabkova, J., Oplustil, S., Gibling, M. R. & Falcon-Lang, H. J. Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided river plain prone to flood disturbance (Nyrany Member, Central and Western Bohemian Basin, Czech Republic). *Rev. Palaeobot. Palynol.* **163,** 153–189 (2010).
59. Clarke, J. T., Warnock, R. C. M. & Donoghue, P. C. J. Establishing a time-scale for plant evolution. *New Phytol.* **192,** 266–301 (2011).
60. Gibling, M. R., Nanson, G. G. & Maroulis, J. C. Anastomosing river sedimentation in the Channel Country of central Australia. *Sedimentology* **45,** 595–619 (1998).
61. Tooth, S. & Nanson, G. C. The role of vegetation in the formation of anabranching channels in an ephemeral river, Northern plains, arid central Australia. *Hydrol. Process.* **14,** 3099–3117 (2000).
62. Tooth, S., Jansen, J. D., Nanson, G. C., Coulthard, T. J. & Pietsch, T. Riparian vegetation and the late Holocene development of an anabranching river: Magela Creek, northern Australia. *Geol. Soc. Am. Bull.* **120,** 1021–1035 (2008).
63. Harwood, K. & Brown, A. G. Changing in-channel and overbank flood velocity distributions and the morphology of forested multiple channel (anastomosing) systems. *Earth Surf. Proc. Land.* **18,** 741–748 (1993).
64. Rodrigues, S., Bréhéret, J.-G., Macaire, J.-J., Greulich, S. & Villar, M. In-channel woody vegetation controls on sedimentary processes and the sedimentary record within alluvial environments: a modern example of an anabranch of the River Loire, France. *Sedimentology* **54,** 223–242 (2007).
65. Abernethy, B. & Rutherfurd, I. D. The effect of riparian tree roots on the mass-stability of riverbanks. *Earth Surf. Proc. Land.* **25,** 921–937 (2000).
66. Dupuy, L., Fourcaud, T. & Stokes, A. A numerical investigation into the influence of soil type and root architecture on tree anchorage. *Plant Soil* **278,** 119–134 (2005).
67. Pollen, N. Temporal and spatial variability in root reinforcement of streambanks: Accounting for soil shear strength and moisture. *Catena* **69,** 197–205 (2007).
68. Hales, T. C., Ford, C. R., Hwang, T., Vose, J. M. & Band, L. E. Topographic and ecologic controls on root reinforcement. *J. Geophys. Res.* **114,** F03013 (2009).
69. Abbe, T. B. & Montgomery, D. R. Patterns and processes of wood debris accumulation in the Queets river basin, Washington. *Geomorphology* **51,** 81–107 (2003).
70. Webb, A. A. & Erskine, W. D. Distribution, recruitment, and geomorphic significance of large woody debris in an alluvial forest stream: Tonghi Creek, southeastern Australia. *Geomorphology* **51,** 109–126 (2003).
71. Francis, R. A., Petts, G. E. & Gurnell, A. M. Wood as a driver of landscape change along river corridors. *Earth Surf. Proc. Land.* **33,** 1622–1626 (2008).
72. Francis, R. A., Corenblit, D. & Edwards, P. J. Perspectives on biogeomorphology, ecosystem engineering and self-organisation in island-braided fluvial ecosystems. *Aquat. Sci.* **71,** 290–304 (2009).
73. Nanson, G. C., Barbetti, M. & Taylor, G. River stabilisation due to changing climate and vegetation during the late Quaternary in western Tasmania, Australia. *Geomorphology* **13,** 145–158 (1995).
74. Brooks, A. P., Brierley, G. J. & Millar, R. G. The long-term control of vegetation and woody debris on channel and flood-plain evolution: insights from a paired catchment study in southeastern Australia. *Geomorphology* **51,** 7–29 (2003).
75. Brown, A. G. Learning from the past: palaeohydrology and palaeoecology. *Freshwater Biol.* **47,** 817–829 (2002).
76. Davies, N. S. & Sambrook Smith, G. Signatures of quaternary fluvial response, Upper River Trent, Staffordshire, UK: A synthesis of outcrop, documentary, and GPR data. *Z. Geomorphol.* **50,** 347–374 (2006).
77. Gran, K. & Paola, C. Riparian vegetation controls on braided stream dynamics. *Water Resour. Res.* **37,** 3275–3283 (2001).
78. Murray, A. B. & Paola, C. Modelling the effect of vegetation on channel pattern in bedload rivers. *Earth Surf. Proc. Land.* **28,** 131–143 (2003).
79. Coulthard, T. J. Effects of vegetation on braided stream pattern and dynamics. *Water Resour. Res.* **41,** W04003 (2005).
80. Tal, M. & Paola, C. Dynamic single-thread channels maintained by the interaction of flow and vegetation. *Geology* **35,** 347–350 (2007).
81. Braudrick, C. A., Dietrich, W. E., Leverich, G. T. & Sklar, L. S. Experimental evidence for the conditions necessary to sustain meandering in coarse-bedded rivers. *Proc. Natl Acad. Sci. USA* **106,** 16936–16941 (2009).
82. Perona, P. *et al.* Biomass selection by floods and related timescales: Part 1. Experimental observations. *Adv. Water Resour.* http://dx.doi.org/10.1016/j.advwatres.2011.09.016 (2011).
83. Edmaier, K., Burlando, P. & Perona, P. Mechanisms of vegetation uprooting by flow in alluvial non-cohesive sediment. *Hydrol. Earth Syst. Sci.* **15,** 1615–1627 (2011).
84. Corenblit, D. & Steiger, J. Vegetation as a major conductor of geomorphic changes on the Earth surface: toward evolutionary geomorphology. *Earth Surf. Proc. Land.* **34,** 891–896 (2009).
85. Buatois, L. A. *et al.* Colonization of brackish-water systems through time: evidence from the trace-fossil record. *Palaios* **20,** 321–347 (2005).
86. Brasier, A. T. Searching for travertines, calcretes and speleothems in deep time: Processes, appearances, predictions and the impact of plants. *Earth Sci. Rev.* **104,** 213–239 (2011).

87. Naiman, R. J., Bilby, R. E. & Bisson, P. A. Riparian ecology and management in the Pacific coastal rain forest. *BioSciences* **50,** 996–1011 (2000).
88. MacNaughton, R. B. *et al.* First steps on land: Arthropod trackways in Cambrian-Ordovician eolian sandstone, southeastern Ontario, Canada. *Geology* **30,** 391–394 (2002).
89. Davies, N. S., Gibling, M. R. & Rygel, M. C. Marine influence in the Juniata Formation (Upper Ordovician, Potters Mills, Pennsylvania): Implications for the history of life on land. *Palaios* **25,** 527–539 (2011).
90. Buatois, L. A., Mangano, M. G., Genise, J. F. & Taylor, T. N. The ichnologic record of the continental invertebrate invasion: Evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity. *Palaios* **13,** 217–240 (1998).
91. Buatois, L. A. & Mangano, M. G. in *Trace Fossils Concepts, Problems, Prospects* (ed. Miller, W. I.) 285–323 (Elsevier, 2007).
92. Labandeira, C. The origin of herbivory on land: Initial patterns of plant tissue consumption by arthropods. *Insect Sci.* **14,** 259–275 (2007).
93. Boucot, A. J. & Janis, C. Environment of the early Paleozoic vertebrates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **41,** 251–287 (1983).
94. Niedzwiedzki, G., Szrek, P., Narkiewicz, K., Narkiewicz, M. & Ahlberg, P. E. Tetrapod trackways from the early Middle Devonian period from Poland. *Nature* **463,** 43–48 (2010).
95. Sues, H.-D. & Reisz, R. R. Origins and early evolution of herbivory in tetrapods. *Trends Ecol. Evol.* **13,** 141–145 (1998).
96. Cascales-Miñana, B. New insights into the reading of Paleozoic plant fossil record discontinuities. *Hist. Biol.* **23,** 115–130 (2011).
97. Cascales-Miñana, B. & Cleal, C. J. Plant fossil record and survival analyses. *Lethaia* **45,** 71–82 (2011).
98. Labandeira, C. C., Beall, B. S. & Hueber, F. M. Early insect diversification: Evidence from a Lower Devonian bristletail from Quebec. *Science* **242,** 913–916 (1988).
99. Labandeira, C. C. Invasion of the continents: cyanobacterial crusts to tree-inhabiting arthropods. *Trends Ecol. Evol.* **20,** 253–262 (2005).
100. Gradstein, F. M., Ogg, J. G., Smith, A. G., Bleeker, W. & Lourens, L. J. A new geologic time scale with special reference to Precambrian and Neogene. *Episodes* **27,** 83–100 (2004).

Acknowledgements
We thank many colleagues for discussion and assistance, especially A. Bashforth, W. DiMichele, R. Dott, H. Falcon-Lang, R. Gastaldo, P. Gensel, M. Rygel, W. Stein and P. Perona. Funding was provided from a Discovery Grant to M.R.G. from the Natural Sciences and Engineering Research Council of Canada.

Author Contributions
M.R.G. and N.S.D. jointly conceived and undertook the study and fieldwork involved. Both authors contributed to the writing of the manuscript and figure construction.

Additional Information
The authors declare no competing financial interests. Reprints and permissions information is available online at http://www.nature.com/reprints. Correspondence should be addressed to M.R.G.