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Tectonic and environmental controls on Palaeozoic fluvial environments: reassessing the impacts of early land plants on sedimentation

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Abbreviated title: Meandering rivers and terrestrialization

Abstract: The apparent increase in occurrence of meandering fluvial channel systems in the Middle Palaeozoic has long been related to the effects of land-plant colonization. However, evidence for meandering channels in non-vegetated settings is shown by pre-vegetation successions on Earth, from the prevalence of meandering channels on Mars, from physical modelling of meandering channels, and from non-vegetated channels in modern desert basins. In addition, early land plants had small dimensions, were limited in their occurrence, and were dependent on environmental factors. Here, we question the capacity of early land plants to impose the major impacts suggested by current models. We propose that the sudden widespread occurrence on Earth of fluvial deposits indicative of the accumulation of meandering river systems in the Middle Palaeozoic was primarily an effect of environmental and tectonic conditions that prevailed during this period. These conditions induced a worldwide increase in the proportion of meandering rivers, which in turn helped propitiate the appropriate environment for land-plant colonization of the continents. We propose that land plants opportunistically took advantage of an appropriate global environment which enabled them to thrive in continental environments. Fluvial environments characterized by single channel systems and stable floodplains facilitated the greening of the land.

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Terrestrialization heralded the colonization of the continents by land plants and animals, and occurred primarily from the Ordovician to the Devonian (Vecoli *et al.* 2010). Early land-plant colonization is considered to be a major cause of fundamental global changes in continental depositional environments in the Middle and Upper Palaeozoic, a situation that has been reported to be particularly pronounced in the fluvial realm, where an increase in the occurrence of inclined heterolithic meandering fluvial system deposits has been reported (Cotter 1978; Davies & Gibling 2010, 2013; Gibling *et al.* 2014). However, early land plants had small dimensions and were limited to geographically restricted wet habitats, linked to mud-prone and heterolithic settings typical of estuarine and fluvio-deltaic environments (Algeo *et al.* 1998; Mintz *et al.* 2010; Labandeira 2007; Kennedy *et al.* 2012); consequently, the magnitude of their influence on channel patterns is uncertain.

Alluvial plain slope and the availability of fine-grained sediments required to provide cohesion to river banks are the major controls of channel planform style (Schumm & Khan 1971, 1972; Peakall *et al.* 2007). Meandering, sinuous channelised fluvial deposits can accumulate without vegetation, where appropriate bank cohesion is provided by fine-grained sediments (Peakall *et al.* 2007; Matsubara & Howard 2014; Matsubara *et al.* 2015). Such systems are recorded from the Neoproterozoic of Scotland (Santos & Owen 2016), and are described from Mars (Burr *et al.* 2009, 2010; Williams *et al.* 2013) and Titan (Burr *et al.* 2013). Although Middle Palaeozoic meandering-channel deposits have been linked to early vegetation, the overall tectonic and environmental settings which accompanied, and may have acted as catalysts for Terrestrialization on Earth, have yet to be fully considered.

A specific set of tectonic and environmental settings was present concomitant to colonization of the continents by land plants. Abnormally high sea levels during the Ordovician, Silurian, and Devonian (200 to >500 m above present-day level) (Hallam 1984; Haq & Schutter 2008) resulted in the development of a series of very large epicontinental marine basins throughout much of what is now North and South America, Africa and Europe (Ronov *et al.* 1976) – a situation which has not occurred again during the later Phanerozoic. Furthermore, the Taconic and Caledonian orogenies promoted overall tectonic settings in which large sea-ways became progressively isolated from global ocean systems (Soper *et al.* 1992; Blakey 2003), leading to the development of long-lived, internally-drained basins (Sobel 2003). Such continental amalgamation at tropical latitudes meant that most continental masses experienced warm climates, which encouraged enhanced rates of chemical weathering and clay production (Nardin *et al.* 2011). These tectonic and environmental conditions, which prevailed during the Middle Palaeozoic, led to the development of sedimentary environments characterised by abundant fine-grained clastic detritus that accumulated on low-gradient slopes.

The aim of this study is to test the hypothesis that it was the specific set of palaeogeographic and tectonic conditions that prevailed during the Middle Palaeozoic, rather than early land plants, that induced the conditions required for the extensive accumulation of fine-grained sediments (and organic matter) in fluvial floodplain and coastal plain palaeo-environments, and in turn drove the increase in the occurrence of meandering fluvial successions. Such abiotic environmental controls may be more likely to have imposed major and geologically rapid changes in patterns of sedimentation than the typically small and geographically restricted early plants that colonized the land in the Late Silurian and Early Devonian. Such conditions may then have promoted the development of meandering channel fluvial systems with stable floodplains under the influence of a warm and wet climate, thereby establishing appropriate conditions for the Terrestrialization event. We review the geological and climatic settings, the palaeontological evidence, and the fossil record of land plants of the Early to Middle Palaeozoic. Further, we provide examples of meandering channel planforms developed in the absence or near-absence of vegetation in modern desert basins. Specific objectives of this work are as follows: (i) to gain an improved understanding of secular changes in sedimentary successions; (ii) to establish the relative roles of tectonic and environmental controls over biogenic activity in stabilizing fluvial floodplains and encouraging meandering river behaviour; (iii) to present modern-day analogues and experimental examples of non-vegetated meandering channels; and (iv) to propose a novel and innovative mechanism with which to account for observed trends in Mid-Palaeozoic fluvial deposits.

Rivers through geological time

Fluvial deposits provide abundant information on the evolution of continental environments through geological time (Bridgland *et al.* 2014). Pre-vegetation fluvial systems encompass a number of distinct fluvial styles, with in-channel bar dynamics similar to modern rivers, and high geomorphic variability (Long 2011, Santos *et al.* 2014, Ielpi & Ghinassi 2015, Ielpi & Rainbird 2015). Examples of published data describing pre-vegetation meandering channel deposits include two stratigraphic levels of the Early Proterozoic Hatches Creek Group in central Australia (Sweet 1988), interpretations of which are based on fining-upward vertical successions with few examples of three-dimensional architectural geometries described. Pretorius (1974) suggested that a meandering channel belt may have developed in proximal-to-middle reaches of fluvial-dominated alluvial fan deposits preserved in the Proterozoic Kaapvaalian sedimentary basins of South Africa, similar to modern-day distributive fluvial systems (Hartley *et al.* 2010). Other examples include sandy meandering fluvial systems, which have been identified in the Serpent Formation (pebbly sandstone deposits) from the Huronian of Canada (Long 1976), in the Neoproterozoic Katherine Group (Long 1978), in the Neoproterozoic Nelson Head Formation (Long 1978; Rainbird & Young 2009), in cobble-grade conglomerates at Ularu (Long 2011), and in sandy-conglomerates in the Borden Basin (Long & Turner 2012). Examples of preserved levee and crevasse-splay elements, and inclined heterolithic strata (*sensu* Thomas *et al.* 1987) associated with laterally-accreting channels, typical of fluvial systems characterized by long-lived floodplains, have been identified in the Neoproterozoic Torridon Group (Fig. 1) (Santos & Owen 2016). This demonstrates that the presence of fine-grained sediments alone could stabilize point bars in pre-Silurian fluvial systems.

Insights from experiments, modern analogues and other planets

Many laboratory-based attempts have been made to simulate the conditions with which to produce self-sustaining meandering channel systems. Slope, bank cohesion and resistance are considered to be the main controls on the formation of highly-sinuous channels (Peakall *et al.* 2007; Braudrick *et al.* 2009; Tal & Paola 2010; Lazarus & Constantine 2013). Flow resistance can be represented by landscape roughness (topography and vegetation density), and its relation with surface slope directly influences river-channel sinuosity (Lazarus & Constantine 2013). Grain-size scaling presents many constraints in flume experiments, particularly the scaling of silt and clay (Peakall *et al.* 1996), but progress on optimising this has been made (Peakall *et al.* 2007; Kleinhans *et al.* 2014). The necessary cohesion required to stabilize river banks and floodplains, and to reduce chute cutoffs, can be achieved in the presence of silt-grade sediments, which can considerably reduce erosion rates (Peakall *et al.* 2007; Van Dijk *et al.* 2013). Furthermore, vegetation alone is not wholly sufficient to induce meandering (Gran & Paola 2001) and, although clay-grade sediments were apparently rare in pre-vegetation times, silt-grade sediments were not (Long 2011).

Analysis of numerous presently active sedimentary basins developed in arid climates can also shed light on the question of whether vegetation is required for meandering channel formation. Non- to poorly-vegetated meandering river systems are evident on Google Earth© imagery. Figure 2 highlights the similarities between meandering channels with and without the presence of vegetation: Figs. 2a and 2b show non-vegetated meander belts developed in the Sahara Desert in Chad and the Aral Sea Basin in Turkmenistan, respectively. These meander belts have similar widths, channel widths and sinuosities (i.e. similar morphological forms) to the meander belt of the Taquari River in the Pantanal wetlands in Brazil (Fig. 2c), which developed with abundant vegetation on both channel and floodplain environment.

The widespread occurrence of meandering channel planforms elsewhere in the solar system may seem paradoxical, with numerous examples from Mars (Schon *et al.* 2012) and also Titan (Burr *et al.* 2013). Outstandingly preserved meandering palaeochannels on Mars are widespread (e.g. Moore 2003; Burr *et al.* 2010; Hoke *et al.* 2014; Irwin III *et al.* 2014; Williams & Weitz 2014; Lefort *et al.* 2014; Peakall 2015), whereas braided palaeochannels have not been confirmed (Ori *et al.* 2013; Matsubara *et al.* 2015; Peakall 2015), with potential examples restricted to alluvial fans within craters (e.g. Palucis *et al.* 2014; Morgan *et al.* 2014). In each of these systems, the cohesion required for bank stability was probably provided by the presence of fine-grained sediments in the overall depositional environments, and this was likely the key control for the development of meandering channel planforms on Mars (Matsubara *et al.* 2015; Peakall 2015). The preservation, retention, and production of fine-grained sediments in alluvial environments can be achieved through various environmental controls, and on Earth this situation is shown to have occurred prior to the greening of the land (e.g. Santos & Owen 2016).

Early land plants and their impacts on sedimentation

Prior to Terrestrialization, continents were not completely barren, but occupied by primitive life forms (Prave 2002; Dott 2003), with a significant volume of biomass present at least since the Palaeoproterozoic (Ohmoto 1996). Microbially-induced sedimentary structures (MISS) have been present in intertidal areas since the Archean (Noffke 2007, 2009), and some authors have proposed microbially colonized land areas during the Proterozoic (Prave 2002). Primitive life forms could not only induce weathering (Astafieva & Rozanov 2012), but could also trap and bind sediments and create mature soil profiles with kaolinitic clays (Retallack & Mindszenty 1994; Dott 2003). MISS are recorded in 1.58 Ga fluvial deposits from the Mukun Basin in Siberia (Petrov 2014), and 1.2 to 0.9 Ga non-marine deposits from the Mesoproterozoic to lower Neoproterozoic Torridonian Sandstones from Scotland (Prave 2002; Battison & Brasier 2012). They still occur in present-day fluvial systems (Schieber *et al.* 2007).

Land plants (i.e. embryophytes) spread initially from Gondwana, and later colonized Avalonia and Baltica (Steemans *et al.* 2009; Gerrienne *et al.* 2010; Rubinstein *et al.* 2010). The oldest embryophytes appeared during the Middle Ordovician (Kenrick *et al.* 2012). They are recorded from heterolithic and muddy sediments deposited in estuarine environments from eastern Gondwana, and presented very-low rates of evolution at least until the early Silurian (Rubinstein *et al.* 2010), as indicated by “bryophyte-like” plant microfossils with probable liverwort affinities (Gray *et al.* 1982; Strother *et al.* 1996; Wellman & Gray 2000; Wellman *et al.* 2003; Steemans *et al.* 2009). The first plants to colonize the continents in the latest Ordovician to earliest Silurian were pre-tracheophyte, embrophytic or bryophytic plants that were intrinsically linked to wet substrates; their evolution progressively helped construct different types of wetlands (Greb *et al.* 2006). Early land plants from the Ordovician and Silurian likely imposed limited impacts on weathering rates and soil formation due to their shallow root systems (Algeo & Scheckler 2010).

The plant body-fossil record begins in the Late Silurian: such fossils are typically a few centimetres in length at most and possess little or no internal structure (Kenrick *et al.* 2012). Land plants occupied coastlines of Late Silurian to Middle Devonian palaeocontinents (Labandeira 2007), simultaneously to the development of ecosystems characterized by plant-animal interactions (Chaloner *et al.* 1991). By the late Lower Devonian (Emsian), land plants had colonized many wet alluvial environments, such as lake margins, wetlands, basin margins, coastal-deltaic settings adjacent to brackish water bodies, and river plains (Kennedy *et al.* 2012), being ecologically restricted to moist environments. They were less than 1.0 m tall, and most likely exercised limited geochemical effects on soils as a result of their limited biomass (Morris *et al.* 2015). Lignophytes (woody plants) rapidly spread from Gondwana in the Lower Devonian, towards Laurussia in the Middle Devonian (Gerrienne *et al.* 2010); they were analogous to tree ferns, and possessed centimetre-long root systems (Algeo *et* *al.* 2001; Meyer-Berthaud *et al.* 2010). Tree habitats were extensive only by the Middle Devonian (Cornet *et al.* 2012; Kenrick *et al.* 2012), and at this time were confined to swampy environments associated with fluvial and deltaic systems, which facilitated water-dependent reproduction (Mintz *et al.* 2010).

Root systems of early land plants were of limited size by the Silurian and Lower to Middle Devonian: they evolved to larger size by the end of the Devonian (Kenrick & Crane 1997; Algeo & Scheckler 2010; Kenrick & Strullu-Derrien 2014). Rhizomes preserved in the Late Silurian (Ludlow) of Pennsylvania penetrated up to 20 cm into the substratum (Retallack 2015). Although Lower Devonian palaeosols record roots and rhizomes generally <10 cm (Gensel & Berry 2001), Hillier *et al.* (2008) described 0.6 m-long root structures preserved in the Lower Devonian of the Anglo-Welsh Basin. Plant-root networks capable of penetrating more than one metre into the substratum evolved concomitantly with the evolution of more complex land plants in the Upper Devonian (Mintz *et al.* 2010; Morris *et al.* 2015), when floodplain forests with complex root networks developed (Algeo *et al.* 1998; Algeo & Scheckler 2010). Although the proportion of plant mass represented by roots increased gradually from the Lower to Upper Devonian (Pragian – Frasnian), vegetated land area increased sharply only during the last stage of the Upper Devonian (Famennian) as a result of plant diversification (Algeo & Scheckler 2010).

The first forests are believed to have developed by the Middle Devonian, and were characterized by tree-fern-like plants (some of which reached up to 8 m height), but characterized by small anchoring roots, developed on sandy mudstone horizons preserved in wetland coastal-plain deposits (Stein *et al.* 2007, 2012). In the Middle Devonian, fossils of water-restricted cladoxylopsid trees provide evidence of the earliest land-plant fossil group with bifacial vascular cambium, which produced wood; these forms were characterized by root systems of limited depth, with typical diameters of 1 to 2 cm; they occupied muddy swamp and boggy environments, and were water-dependant for reproduction (Driese *et al.* 1997; Mintz *et al.* 2010; Stein *et al.* 2012). The first cladoxylopsid forests developed in deltaic and tidal environments (Cornet *et al.* 2012). They were followed during the Givetian (upper Middle Devonian) by Archaeopteridales, which spread from Laurussia and developed forests in tropical fluvial floodplains near palaeoshorelines; these forms were characterized by roots up to 1.5 m long, and had horizontally extended deciduous branches (Driese *et al.* 1997;

Meyer-Berthaud *et al.* 1999; Bridge 2000; Mintz *et al.* 2010; Cornet *et al.* 2012). The fossil record of the first forests, from the Early and Middle Devonian, is mostly restricted to freshwater near-channel deposits developed in subtropical-to-tropical palaeoclimates as a result of peculiar continental configuration (Edwards & Fanning 1985; Greb *et al.* 2006; Berry & Marshall 2015).

Terrestrialization through the Middle Palaeozoic fluvial rock record

It is important to highlight that braided and meandering morphologies are just end-members of a continuum of fluvial-channel planform types (Bridge 2003). Distinctions between straight and meandering channel are generally not process-based, and the characterization of river types through planform alone is potentially inadequate (Carling *et al.* 2014). Meandering is a mature channel planform style, mostly related to a combination of process-controlling factors such as discharge, sediment input, alluvial plain gradients, and bank stabilization (Smith *et al.* 1989). Flume experiments have highlighted that variations in slope and availability of fine-grained sediments (cohesion) are major controls of channel planform style (Schumm & Khan 1971, 1972; Peakall *et al.* 2007): slope is not dependent on the presence of vegetation, and fine-grained deposits are not exclusively dependent on vegetation, although their preservation can be enhanced by the presence of the latter.

The idea that land-plant colonization drove important changes in the dominant type of fluvial system accumulation and preservation from the Silurian and Devonian periods was originally inspired by the work of Schumm (1968), and further developed by other workers (e.g. Cotter 1978; Davies & Gibling 2010; Davies *et al.* 2011; Gibling *et al.* 2014; Corenblit *et al.* 2015; Almeida *et al.* 2016). Databases on Palaeozoic fluvial deposits (Cotter 1978; Davies & Gibling 2010) show a trend of a preferential occurrence of meandering channel systems from the Middle to Late Palaeozoic, which these researchers link to the effects of the greening of the land. This situation has led to the establishment of a number of paradigms regarding pre-vegetation fluvial systems, and the impacts of early vegetation on continental sedimentation. A marked increase in the occurrence of preserved palaeosols, thick muddy floodplain deposits, and sets of inclined heterolithic stratification is recorded for Silurian-Devonian fluvial settings (Cotter 1978; Davies & Gibling 2010; Gibling *et al.* 2014). The earliest Palaeozoic heterolithic succession described in the literature to date is in the Ordovician, whereas the first record of lateral-accretion sets (Fig. 3) is close to the Silurian-Devonian boundary (Davies & Gibling 2010). More recently, the latter database has been expanded to include the Carboniferous period, and the anastomosing fluvial style (Davies & Gibling 2013; Gibling *et al.* 2014). We exclude the anastomosing interpretations in Fig. 3 to keep the original distinction of just the two end-member fluvial styles: braided and meandering.

Palaeozoic environment

A predominantly alkaline atmosphere prevailed between the Ordovician and Silurian, with the highest pH levels recorded in the entire geologic record (Jutras *et al.* 2009). High pH levels increase silicate mineral dissolution, similarly to low pH levels (Drever 1994). The Ordovician Taconic orogeny and the Silurian to Early Devonian Caledonian continental amalgamation, and associated tectonic plate movements, promoted a palaeogeographic setting where most of the continents (with the exception of Gondwana) occupied intertropical convergence zones that were subject to warm and humid climatic conditions with high rates of rainfall. This resulted in enhanced rates of chemical weathering (Nardin *et al.* 2011; Lenton *et al.* 2012). Furthermore, average rates of sedimentation are enhanced in the initial and final stages of tectonic cycles: an increased rate of accumulation of sediment is recorded in the Devonian (Fig. 4) as a response to the Caledonian Orogeny (Ronov *et al.* 1980).

A large area of the continental landmasses (35–47%) was inundated by the sea (Fig. 4) between the Ordovician and the end of the Devonian (Ronov 1994). From the eustatic lowstand at the beginning of the Cambrian (Fig. 3), eustatic sea level progressively rose, and in the Middle Ordovician to Late Devonian the highest long-term eustatic sea level of the Phanerozoic is recorded (Hallam 1984; Haq & Schutter 2008), with shallow-marine inundation of many continental basins (Ronov 1994). The maximum recorded transgression of the Phanerozoic occurred in the Late Ordovician, with a second maxima recorded in the Middle-Late Silurian (Fig. 3), related to the Caledonian orogenic cycle (Ronov *et al.* 1980). Ordovician to Devonian deposits from Gondwana basins (e.g. the Paraná, Parnaíba, and Amazonas basins in Brazil, the Central Basin in Zaire, the Cape Supergroup in South Africa, and the Carnarvon Basin in Australia) are dominated by marine, shallow marine, and coastal deposits.

Large Ordovician epicontinental seas and their shorelines progressively retreated leaving emergent low-lying coastal plains in the Silurian (Weller 1898), and exposure of large areas of marine, fine-grained deposits. The culmination of continental assemblage resulted in narrow oceans and relatively short distances between palaeocontinents in the early Silurian, as recorded by close similarities of miospore-assemblages between the Gondwana, Avalonia and Laurentia palaeoplates (Steemans & Pereira 2002). A globally pronounced intense weathering event due to CO_2 decrease resulting from continental motion through intertropical zones is recorded concomitantly with the start of the Terrestrialization during the Ordovician (Nardin *et al.* 2011). Sea-ways were progressively dammed, and many endorheic (internally-drained) basins formed, as recorded, for example, by numerous examples of terminal fan deposits in Devonian basins from England, Ireland, Greenland, and Spitsbergen (e.g. Friend & Moody-Stuart 1972; Kelly & Olsen 1993; Williams 2000). This is recorded in the Old Red Sandstone magnafacies of the British Isles and Scandinavia, which comprises Silurian to Carboniferous successions of the North Atlantic borderlands, and records the sedimentary response to the Caledonian, Ellesmerian, and Variscan orogenies. The Old Red Sandstone magnafacies marks the transition from marine Lower Palaeozoic sedimentation to continental Middle Palaeozoic sedimentation (Friend *et al.* 2000). The Lower Old Red Sandstone was deposited under the influence of a warm to hot climate, and it is a key stratigraphic section from which global interpretations regarding terrestrialization (e.g. Davies & Gibling 2010; Gibling *et al.* 2014) were made. Of significance, the Old Red Sandstone also records many classic examples of lateral accretion sets (so-called epsilon cross-bedding of Allen 1963), some of them (e.g. the Red Marls Group, Late Silurian) are interpreted by Davies *et al.* (2011) as being the oldest known examples in the Palaeozoic of laterally-accreting macroforms of fluvial origin with inclined heterolithic stratification. The Lower Old Red Sandstone deposition occurred in littoral and littoral-related environments, and changes in relative sea levels were fundamental in governing fluvial dynamics recorded by such deposits (e.g. Boyd & Sloan 2000; Hillier 2000). Land-plant fossils are there preserved as allochthonous fragments present in channel deposits (Edwards & Fanning 1985).

Prominent examples of the earliest forests recognised in the rock record are recorded from Middle Devonian deposits of the Catskill magnafacies, particularly in finer-graded fluvial and deltaic successions (e.g. Driese *et al.* 1997; Mintz *et al.* 2010).

River-channel styles in the latter magnafacies of the Middle-Upper Devonian Appalachian foreland basin of New York changed dramatically with distance from palaeoshoreline, with braided-channel styles dominating inland in upstream parts of the succession, and highly sinuous, single channel types with extensive muddy floodplains dominating closer to the palaeo-coast, where such forms occur adjacent to sandy and muddy tidal flats, muddy interdistributary bays, lakes, and tide-influenced channels (Gordon & Bridge 1987; Willis & Bridge 1988; Bridge 2000). The concentration of many datasets of published studies on Palaeozoic fluvial deposits are largely based on the Catskill and Old Red Sandstone magnafacies, and this has resulted in a bias whereby these particular periods are represented by a markedly limited range of depositional settings that are notably characterized by meandering channel systems.

Discussion

An extraterrestrial paradox?

The outstanding meandering palaeodrainage patterns preserved on Mars demonstrate that meandering channels can develop despite the absence of vegetation (e.g. Matsubara *et al.* 2015), and such conditions were met in pre-vegetation Earth (Santos & Owen 2016). The geomorphic expressions of Martian examples of meandering-channel planform are typically characterized by inverted relief (Pain *et al.* 2007), whereby coarser-grained in-channel deposits, that are more resistant to weathering and erosion, are preserved as features with positive relief, whereas the less resilient overbank fines are eroded by aeolian winnowing. In the case of pre-vegetation fluvial deposits, such differential erosion might have played an important role in sediment preservation, as for channel deposits on Mars (see Matsubara *et al*. 2015), masking the original depositional signatures of such systems. On Earth, meandering systems that have been preferentially preserved are those that accumulated in less tectonically active settings, such as stable cratons (Eriksson *et al.* 2006), but which were also more prone to differential erosion of finer-grained sediments during long episodes of terrain denudation (e.g. Williams *et al.* 2009).

Production and preservation of fine-grained sediments

The abundance of mudrocks and their metamorphic equivalents in all continental and marine sedimentary environments is apparently constant through Archean, Proterozoic and Phanerozoic Eons (Ronov 1964). Production of fine-grained sediments and clays could be enhanced by microbial associations well before terrestrialization (Ohmoto 1996; Dott 2003). Fine-grained sediment can accommodate abundant organic matter (carbon and nutrients), as a result of adsorption onto grains, and of similar densities (Mayer 1994). Clay formation from biotic soils predates complex terrestrial ecosystems (Kennedy & Droser 2011), and the weathering products of mafic rocks generate significant mud content (Cox & Lowe 1995). Models indicate that chemical weathering rates in pre-vegetation environments were not significantly different to modern-day ones (Keller & Wood 1993), and some suggest that microbially-induced weathering is only an order of magnitude less effective than land-plant induced weathering (Schwartzman & Volk 1989). Additionally, the recorded high pH levels during the Middle Palaeozoic (Jutras *et al.* 2009) substantially increased weathering rates, thereby yielding larger volumes of fine-grained sediment. Geochemical data indicate a major change in chemical weathering and a rapid increase in clay mineral formation and deposition in the Neoproterozoic, suggesting an already widespread occurrence of primitive biota on land, with clay-forming biotic soils (Kennedy *et al.* 2006).

Several mechanisms that preserve floodplain deposits and fine-grained sediments in non-vegetated systems have been proposed (e.g. Winston 1978; Fralick & Zaniewski 2012; Marconato *et al.* 2014; Santos & Owen 2016). Yet the majority of pre-vegetation fluvial systems described in the literature are characterized by a paucity of such sediments (Long 2011). The bypass of fine-grained sediments to distal areas of a basin as a result of a lack of vegetation cover is a possible mechanism (Long 1978; Winston 1978; Eriksson *et al.* 1998; Santos *et al.* 2014), as is post-depositional aeolian winnowing (Dalrymple *et al.* 1985). Given appropriate conditions, pre-vegetation fluvial systems could preserve fine-grained sediments and depositional architectures similar to post-vegetation deposits, including inclined heterolithic strata and laterally accreting channel deposits (Santos & Owen 2016). Source-area lithology is a fundamental control on sediment type (Assine *et al.* 2015) but is rarely discussed. As an example, sedimentary deposits of the modern Taquari megafan from the Pantanal wetlands in Brazil are characterized almost solely by fine-grained sand (Assine 2005), and the resulting preserved sedimentary facies are homolithic, despite being deposited in a densely vegetated wetland (Fig. 2c).

Tectonics and environment as major depositional controls during the Palaeozoic

The coupling between geomorphic and biological processes results in feedback that can promote what can be considered as evolutionary geomorphology, where vegetation and earth surface processes conspire to influence the evolution of landforms (Corenblit & Steiger 2009). However, tectonics, climate, sediment flux, atmospheric and water body productivity, and sea level remain the primary controls on sedimentary environment development, despite the feedbacks provided by biogenic processes (Leeder 2007). This situation was consequently more pronounced in the Precambrian and in the initial phases of terrestrialization, from the Ordovician to the Devonian. The relative abundance of meandering river deposits in comparison with braided river deposits can also vary as a consequence of climate and tectonic controls (Michaelsen 2002; De La Horra *et al*. 2012).

The nature of climate, oceanic currents, atmospheric composition, and, particularly, of the position of global landmasses, changed considerably throughout the Phanerozoic, meaning that a uniformitarian approach is not necessarily applicable to interpretations of sedimentary trends in the rock record (Bateman *et al.* 1998). The sedimentary rock record is biased by the preservation of particular geomorphic features, such as sedimentary basins, which are not necessarily an ideal representation of the past (Nyberg & Howell 2015). Alluvial environments are largely controlled by tectonics and eustatic sea levels in modern-day basins (Weissmann *et al.* 2010). Large-scale sea-level changes alter the relative predominance of sedimentary environments (Peters 2006; Smith & McGowan 2011). Critically, transgressive and highstand system tracts are the times during a sea-level cycle when maximum rates of fluvial sedimentation and accumulation occur (Wright & Marriott 1993; Colombera *et al.* 2013).

The development of large epicontinental seas and internally-draining basins as a consequence of the Caledonian continental amalgamation from the Ordovician-Devonian period (Fig. 5) contributed to an increase in the proportion of preserved fine-grained sediments: internally-draining basins significantly enhance the likelihood of preservation of mud-prone deposits (Nichols & Fisher 2007). A transition from the preferential accumulation of coarse-grained to finer-grained fluvial strata is coincident with the timing of maximum marine incursion (i.e. the Maximum Flooding Surface) into alluvial-plain environments (Shanley & McCabe 1991). This increase in fine-grained strata occurs due to an increase in the rate of creation of accommodation space and the opportunity for rapid vertical accretion of fluvial successions to fill that space

(Wright & Marriott 1993; cf. Colombera *et al.* 2015). Base-level rise also reduces valley slope (i.e. the average gradient of the fluvial profile) and, when coupled with the reduction in sediment grain calibre, tends to favour a transition from a braided fluvial pattern to a meandering pattern (Bridge & Leeder 1979), with a high proportion of the alluvial plain becoming river-dominated and floods more commonly reaching the interfluves (Allen 1974). A long-term, sustained rise in base level favours the accumulation of thick successions of fluvial deposits (Shanley & McCabe 1994; Nichols & Fisher 2007). Transgressive- to highstand-system tract deposits tend to be characterized by isolated, meandering channel-fill deposits arranged into stacked fining-upward successions, each separated by thick, mud-prone floodplain deposits (Shanley & McCabe 1991). The prolonged global sea-level highstand during the Middle Palaeozoic had major impact on continental sedimentation and changed fluvial base levels, leading to a reduction in overall gradient in the distal reaches of many large rivers, thus encouraging these systems to adopt a meandering, low-gradient morphological form in their lower reaches (Fig. 5). Such transition from marine to continental sedimentation is recorded in the Siluro-Devonian Lower Old Red Sandstone of the UK (Hillier & Williams 2004), where the influence of relative sea level, climate, and overall tectonic settings were potentially more important in determining preserved depositional architecture and on the production and preservation of fine-grained sediments than the impact of early land plants.

The recorded weathering conditions during the Middle Palaeozoic led to higher rates of clay generation and consequent input of such sediments into alluvial systems. Large areas covered with fine-grained sediments were exposed as low-lying, low-gradient plains (Weller 1898), after a long period of marine inundation of the continental shelves in the Silurian. This environmental setting was unusual, although the Precambrian rock-record is considerably less representative due to rock-recycling events and lithological characteristics, meaning that such settings could have occurred before but as yet remain unrecognized. As a result of the continental assemblage in the intertropical convergence zones during the Middle Palaeozoic, high rates of rainfall coupled with warm climates resulted in an environmental setting suitable for water-dependant land-plant establishment, further increasing weathering rates (Nardin *et al.* 2011; Lenton *et al.* 2012). The relationship between palaeogeographical settings and evolution, through speciation and diversification, has also been proposed as a major driver of angiosperm diversification in the Late Jurassic and Early Cretaceous (Buerki *et al.* 2014).

Meandering channels and land plants: the chicken and the egg

The current paradigm suggests that early land plants led to a rapid rise in meandering channels. However, mechanisms to induce the stabilization of single channels were present before terrestrialization, and meandering fluvial systems did develop prior to the evolution of land plants (e.g. Pretorius 1974; Sweet 1988; Long 2011; Santos & Owen 2016). Furthermore, processes to produce clay sediments and clays were present at least by the Palaeoproterozoic, and the volume of mudrock apparently did not vary considerably through geological times. The presence of a widespread biota by the Neoproterozoic would also affect bed roughness and promote fine-grained sediment retention and production, thereby reducing runoff rates and enhancing cohesion of fluvial systems. The transition from microbial to early land-plant ecosystems suggests that the impact of early land plants was unlikely to have been as pronounced as previously envisaged since early land plants exerted influences similar to those of earlier continental life forms. The presence of microbes, and the environmental conditions that encouraged them to flourish, assisted land-plant colonization. Not only can microbial action induce weathering, but most of the chemical weathering induced by root systems comes from the symbioses between roots and mycorrhizal fungi (Jongmans *et al.* 1997; Kenrick & Strullu-Derrien 2014).

Early land plants are mostly associated with fine-grained sediments (Elick *et al.* 1998), implying that such life forms required the presence of such sediment types (or organic matter accumulation) to become established. Ordovician-Devonian land plants could not supplant major controls on alluvial stratigraphy such as aggradation rates, sediment input, alluvial plain surface gradients, and base level, in a relatively short period of time (the end of the Silurian and the early Devonian). These plants, with their shallow anchorage systems, were not capable of inducing marked increases in rates of weathering to produce the observed increased preservation of fine-grained sediments (e.g. Cotter 1978) since they were at least ten times less effective than later trees (Kenrick & Strullu-Derrien 2014; Quirk *et al.* 2015). The constant need for, and adaptations to retain, water by early land plants indicates that they were not sufficiently resilient to overcome difficulties imposed by the environment; shallow root systems meant they were less resistant to drought, for example. As recorded by fossil occurrences, early land plants were intimately associated with swamp, deltaic and floodplain environments. Although the greening of the land unquestionably represents an important event in the evolution of continental landscapes, most of the depositional controls with which to induce meandering channels were present before the Silurian and Devonian. Meandering river environments, with their stable single-thread channels on low-gradient plains and stable floodplains on which fine-grained sediments and organic matter could accumulate, are the most appropriate continental environment type for sessile organisms to thrive. Conversely, a braided river environment with multiple, highly mobile channels and coarse-grained floodplains would be sub-optimal for initial colonization. Early land plants may have required meandering fluvial systems and their extensive floodplains to become established, rather than being the primary cause of their presence.

We propose that the combination of extensive epicontinental and internal drainage basins, land masses in intertropical convergence zones, high sea levels, low slope gradients, and a period of intensive weathering, was the primary cause of the observed systematically increasing occurrence of fluvial deposits containing mudrock (Fig. 4) and inclined heterolithic strata from the Silurian to the Devonian, particularly in deposits from Europe and North America. These fine-grained sediments promoted the necessary cohesive forces and gradients required to stabilize the substrate of alluvial plains. The presence of extensive floodplains facilitated the establishment of appropriate settings for early land plants and their fragile root systems. It may be that the environmental impact of land plants was able to homeostatically sustain such appropriate conditions.

Conclusions

The dimensions of Silurian to early Devonian land plants, in particular their root systems with limited penetration depth, corroborates the idea that the observed impacts on the Middle Palaeozoic fluvial realm are most likely dominated by allogenic processes. These include environmental and tectonic conditions, such as high eustatic sea level, low-gradient alluvial plain slopes, orogenic cycles, high weathering rates as a result of elevated pH conditions, the widespread development of endorheic basins, and the location of continental landmasses in intertropical latitudes. This worldwide context, which has not occurred again since, induced the widespread development and unusual dominance of meandering channel fluvial system types. These settings may have provided the appropriate environment for the onset of the colonization of the continents by land plants. The interpretation of plants as the dominant control on sedimentation from the time of their first evolutionary stages is unrealistic. Land plants were not the primary cause of the apparent peaks in occurrences of meandering channel fluvial systems. In contrast, the evolution and appearance of different types of embryophytes since the Middle Palaeozoic – notably angiosperms in the Mesozoic – have exerted various different impacts on modern sedimentary environments. The changing impacts of land plants on sedimentation must be understood as a series of gradual steps during a longer time frame. We suggest that the impacts of early land plants on fluvial systems have been overstated, and were less influential than the current paradigm envisages. We suggest that land plants may have taken an evolutionary advantage of fortuitous environmental conditions, and developed ways with which to impose a feedback onto the environment, sustaining, as geo-engineers, a situation whereby river plains and dynamics became buffered and less energetic, resulting in the establishment of homeostasis (Fig. 6).

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Figures captions

Fig. 1. Examples of inclined heterolithic deposits from the Neoproterozoic Torridon Group (Allt na Béiste Member of the Applecross Formation). (**a**) Channel deposits encased by fine-grained, floodplain deposits. Two fining-upward successions are present, and levee deposits can be identified (at the level of the legs of person as scale), and dip to the left of the picture. These are overlain by lenses of crevasses and overbank fines. (**b**) Point bar deposits with inclined heterolithic strata. See Santos & Owen (2016) for further details. SB, sandy bedforms; CV, crevasse deposits; LV, levee deposits; FF, floodplain fines; IHS, inclined heterolithic stratification. White arrow at the upper right of (b) indicates direction of accretion.

Fig. 2: Comparison between non-vegetated meander belts developed laterally to dune fields, at the Sahara Desert in Chad (a) and at the Aral Sea Basin at Turkmenistan (b), with abundantly-vegetated meander belt developed on modern wetland, at the Pantanal

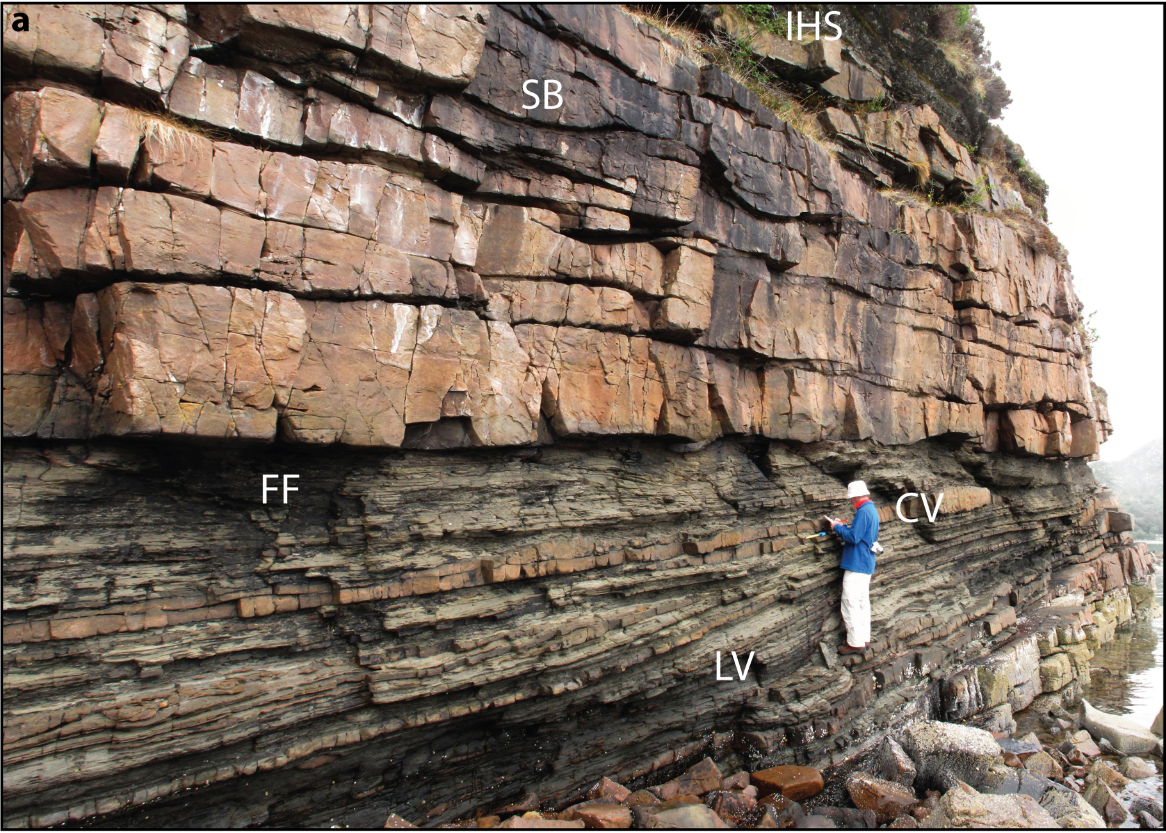
Basin, central-west Brazil (c). Flow to left in all examples. Black arrows indicate scroll preservation. Black bars at upper left are 2 km long.

Fig. 3. Meandering river deposits, mean sea-level curves, and plant root depths, throughout the Phanerozoic. Eustatic curves (adapted from Haq & Schutter 2008) of the Palaeozoic (**a**) and the percentage of interpreted meandering river deposits (**b**) described in the literature (modified from Gibling *et al.* 2014). The mean sea-level curve is relative to present day sea-level (0 m).". (**c**) Land plant root-depth evolution during the Palaeozoic; values relate to maximum root-depth in metres (Hillier *et al.* 2008; Kahmann & Driese 2008; DiMichele *et al.* 2010; Giesen & Berry 2013, Morris *et al.* 2015; Retallack 2015). Geological ages are shown above the graphic: Carb. (Carboniferous); Dev. (Devonian); Sil. (Silurian); Ord. (Ordovician); Camb. (Cambrian).**Fig. 4.** Epicontinental seas, mud-prone fluvial successions, and rates of sediment accumulation. Graph shows the relationship between (**a**) the average rates of sediment accumulation (m/10^6 years) within geosynclines, platforms and continents as a whole (Ronov *et al.* 1980), (**b**) the area (in 10^6 km^2) of continents covered by seas (Ronov 1994), and (**c**) the percentage of published papers describing fluvial successions containing >10 % of mudrock (modified from Davies & Gibling 2010).

Fig. 5. Evolution of continental environments from the Cambrian until the Devonian. Below each palaeoenvironmental reconstruction is shown the palaeogeographic reconstruction of the tectonic configuration of the continents (Blakey 2003). Scale in the right of each period shows mean sea-level curves of each period (Hallam 1984) in metres relative to current levels. Notice that meandering rivers and fine-grained sediment abundance increases before land plant colonization, which we argue herein utilized such environmental configuration to facilitate their spread throughout the

continents. Palaeocontinents: Gond. = Gondwana; Laur. = Laurasia; Laurus. = Laurussia; Sib. = Siberia; and Balt. = Baltica.

Fig. 6. Schematic flow-chart showing the inter-relationship between meandering rivers and land plants. The synergistic relationship between meandering rivers and land plants is shown in red, representing features that are the result of that interaction and which propitiate not only the appropriate environment for vegetation, but also the increasing occurrence of meandering river deposits after the Devonian.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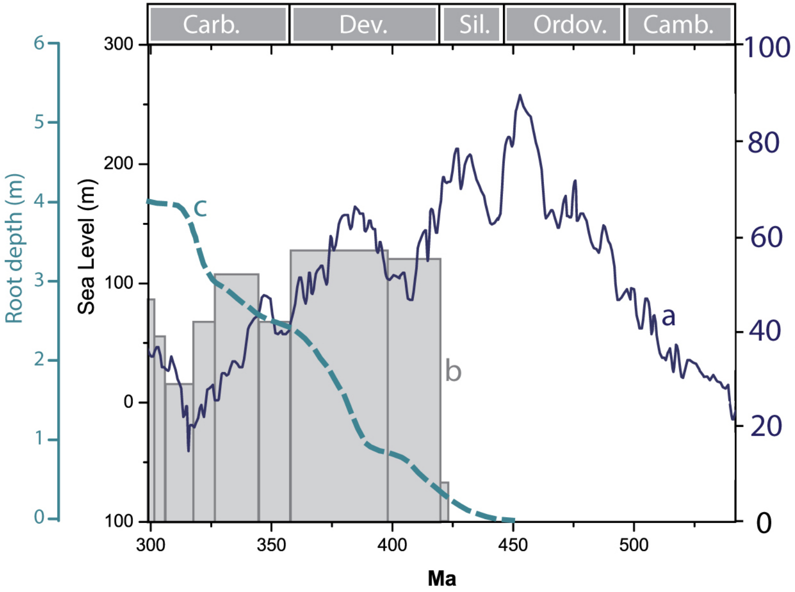
Carb.
Dev.
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Root depth (m)
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5
4
3
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Sea Level (m)
300
200
100
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Meandering river deposits (%)
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a
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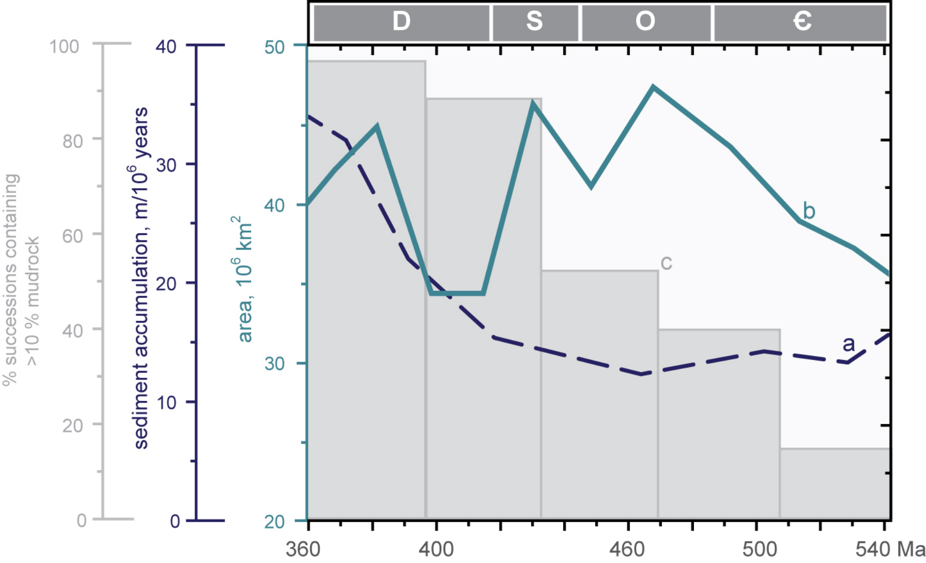
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% successions containing >10 % mudrock
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sediment accumulation, m/10^6 years
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360
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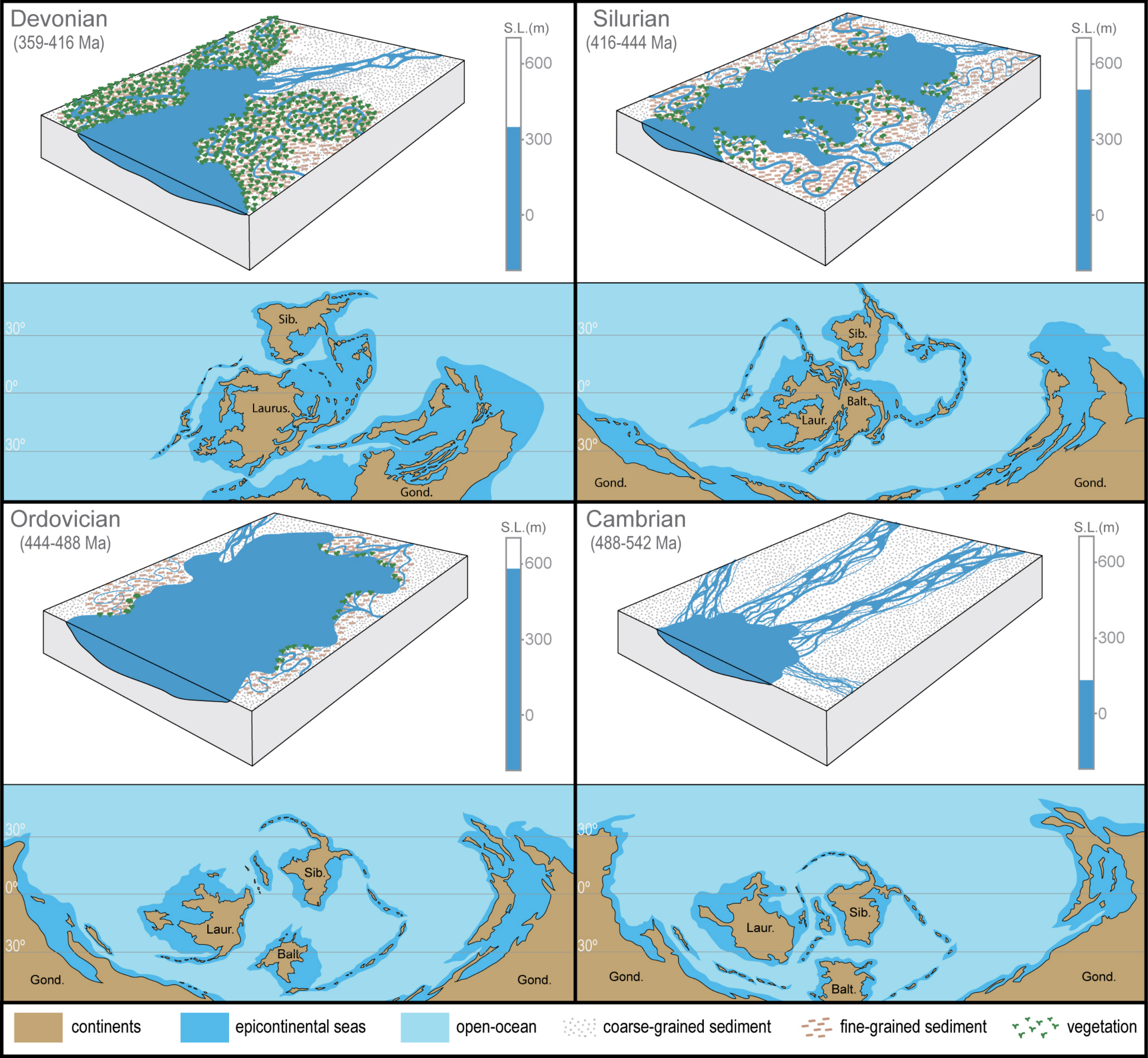
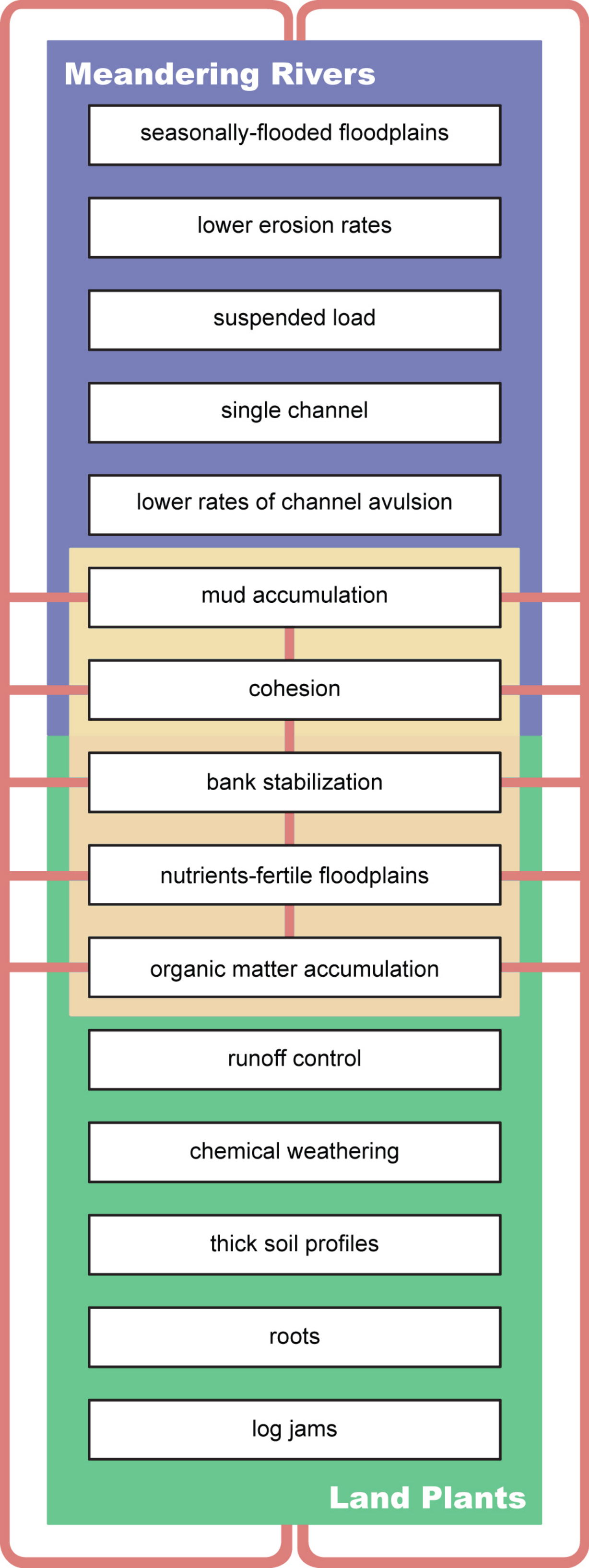
500
540 Ma



Devonian
(359-416 Ma)
S.L.(m)
600
300
0
30º
0º
30º
Sib.
Laurus.
Gond.
Silurian
(416-444 Ma)
S.L.(m)
600
300
0
30º
0º
30º
Sib.
Balt.
Laur.
Gond.
Gond.
Ordovician
(444-488 Ma)
S.L.(m)
600
300
0
30º
0º
30º
Sib.
Laur.
Balt.
Gond.
Gond.
Cambrian
(488-542 Ma)
S.L.(m)
600
300
0
30º
0º
30º
Laur.
Sib.
Balt.
Gond.
Gond.
continents
epicontinental seas
open-ocean
coarse-grained sediment
fine-grained sediment
vegetation


Meandering Rivers
seasonally-flooded floodplains
lower erosion rates
suspended load
single channel
lower rates of channel avulsion
mud accumulation
cohesion
bank stabilization
nutrients-fertile floodplains
organic matter accumulation
runoff control
chemical weathering
thick soil profiles
roots
log jams
Land Plants