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1 **Reply** to Discussion on 'Tectonic and environmental controls on Palaeozoic

2 fluvial environments: reassessing the impacts of early land plants on

3 sedimentation'.

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9 Introduction

We thank Davies et al. (2017) for their Comments and welcome the opportunity to further discuss the 10 11 role of early land plants on fluvial environments. Critically, Davies et al. (2017) note that although testable hypotheses exist for the possible role of early land plants, they remain untested, and thus there 12 13 is correlation (between an increase in meandering systems and early plants) without any mechanistic 14 causation. In Santos et al. (2017) we challenged this causation, offering an alternative mechanism for increasing meandering channels based on a unique set of tectonic and environmental controls. It is 15 important to be clear that Santos et al. (2017) focused on this meandering transition and the possible 16 17 role of early land plants. Davies et al. (2017) conflate our comments regarding the impacts of early 18 land-plant evolution with the longer-term influence of vegetation; there is little doubt over the longer-19 term role played by vegetation, particularly in stabilizing deeply rooted soils. Fluvial sedimentary 20 successions are strongly influenced by tectonics, climate, sediment flux and sea level, and we question 21 whether early land plants of limited size and restricted occurrence were able to dominate over such 22 controls during terrestrialization (cf. Leeder 2007). We maintain our principal argument that a series of abiotic factors conspired to induce a worldwide increase in the proportion of meandering rivers, which 23 24 in turn favoured development of an environment appropriate for land-plant evolution and colonization 25 of the continents.

Davies et al. (2017) raised three main issues: 1) Palaeogeographic setting; 2) Meandering without
vegetation; and, 3) Early terrestrial life. Here we address these successively.

28

29 1) Palaeogeographic setting

30 Davies et al. (2017) argue that tectonic, sea-level and environmental conditions are cyclical, and thus 31 abiotic controls cannot account for the "unidirectional singularity" of the Mid-Palaeozoic Facies Shift (PFS). This argument conflates the initiation of the PFS with the subsequent evolution of plants. We 32 33 argue for a two-phase process: first, tectonic and environmental influences provided appropriate conditions for the accumulation of extensive fine-grained sediments on low-gradient coastal plains; in 34 35 turn, this provided optimal conditions for increased river bank stability and thereby the growth of meandering channels. These conditions, in turn, aided plant terrestrialization by providing ideal 36 37 growing conditions. Later evolution of plants led to much deeper roots (Algeo & Scheckler 2010; Kenrick & Strullu-Derrien 2014; Santos et al. 2017), which provided significant additional bank 38 stability and led to a semi-permanence of this facies shift. However, after several major mass extinctions 39 40 there are abrupt shifts between meandering and braided states (Ward et al. 2000; Retallack et al. 2006; De la Horra et al. 2012); thus the shift to meandering occurs multiple times and is bidirectional. Cyclical 41 42 abiotic controls may be responsible for examples of meandering river deposits prior to the PFS, though 43 there could be no positive feedback encouraging greening of the continents and an enduring facies shift.

Furthermore, the low percentage of rocks preserved in earlier successions makes any such transitions

difficult to assess (Blatt & Jones 1975).

We have highlighted the predominance of equatorial, orogenic, Euramerican studies to support the PFS, and, to our knowledge, examples of muddy overbank fines in other regions are limited to two, both of which are marine-influenced and were associated with high sea level (Hunter & Lomas 2003; Xue et al. 2016), further supporting our model. Our decision to cite data that pre-date the plate tectonics paradigm was deliberate: the information from Weller (1898) relates to sea-level variations not tectonics, and demonstrates the long-recognised significance of the highest eustatic sea level of the Phanerozoic.

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54 2) Meandering without vegetation

56 Davies et al. (2017) question our use of abiotic meandering experiments while admitting they form, and 57 change the question from what do experiments tell us about the key drivers on meandering river 58 development, to what is the role of vegetation in flumes? Vegetation in flumes has been shown to aid 59 the formation of single-thread rivers (Tal & Paola 2007; Braudrick et al. 2009), though in the absence 60 of fines then these were at best wandering (Neill 1973) or irregularly sinuous channels (Desloges & Church 1989). However, it is critical to note that the root depths in these experiments exceeded the 61 62 depth of the channels (see Gran & Paola 2001), thus simulating riparian trees rather than early land plants. These root networks provided increased bank stability that was key to the development of these 63 single-thread channels (Tal & Paola 2007; Braudrick et al. 2009). The shift towards a meandering state 64 in the experiments confirms field observations and numerical modelling that suggest the braiding-65 66 meandering threshold is associated with rooting depths similar to the channel depth (Beechie et al. 67 2006; Eaton & Giles 2009). Additionally, Coulthard (2005) performed similar experiments with 68 sparsely distributed shrub-like vegetation, and reported increased braiding indices. Thus, the 69 introduction of vegetation may not only cause the development of meandering but may also exacerbate braiding (Coulthard 2005). Consequently, the vegetated meandering experiments are far more 70 71 comparable with Late Devonian and younger systems where roots are deep and provide significant bank 72 stability. In contrast, early land plants with shallow and simple root systems (e.g. Retallack 1997) would 73 not have contributed significantly to river bank strength, and may have acted to reinforce braiding. Furthermore, we note that the only experiments which have successfully accumulated inclined 74 75 heterolithic strata (IHS) did not use vegetation (Peakall et al. 2007; Van de Lageweg et al. 2014), thus 76 demonstrating that vegetation is not required for the formation of IHS.

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78 Davies et al. (2017) raise a series of points about our analysis of meandering without vegetation. 79 Curiously, meandering planforms as observed on Mars, Titan, and in our satellite imagery of desert 80 channels, as well as early examples of IHS on Earth, are all considered inadmissible as evidence to 81 support our argument for abiotic meandering at the Mid-Palaeozoic PFS. These studies are dismissed in terms of differences in fluid dynamics (Titan); the absence of ground-truthing from a rover (Mars); 82 the lack of sedimentary cross-sections (planforms of desert systems); the relative paucity of preserved 83 84 early Earth examples of IHS; and by changing the nature of the question to one focused on vegetation, with regard to the experiments (see above). However, it remains the case that all of these examples 85 demonstrate that vegetation is not required for the formation of meandering channels. In sharp contrast 86 87 to this array of evidence for meandering in the absence of vegetation, no study has ever demonstrated a 88 meandering channel that is primarily controlled and stabilised by plants with small rootlets relative to channel depth. In fact, as discussed previously, the opposite is true, with field, experimental, and
numerical evidence that the braiding-meandering transition is associated with rooting depths similar to
the channel depth (Gran & Paola 2001; Beechie et al. 2006; Tal & Paola 2007; Braudrick et al. 2009;
Eaton & Giles 2009).

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3) Early terrestrial life:

97 Davies et al. (2017) note that "it is presently uncertain exactly how primitive land plants, with apparently only limited root-like organs, forced the PFS". Furthermore, Davies et al. (2017) suggest 98 99 that there are several hypotheses for the influence of early land plants, but these are all untested. Here we examine the three hypotheses: 1) plants acted to bind floodplains, potentially due to preservation of 100 dead roots as floodplains aggrade; 2) plants acted as baffles trapping fines; or, 3) plants aided the 101 102 production of fine-grained sediment. Interestingly, all of these hypotheses revolve around the 103 construction of fine-grained floodplains with the accumulation of dead roots as the only possible direct 104 role of early land plants in providing bank stability. On this latter point however, in modern rivers, bank stability is highly dependent on the ratio between rooting depth and bank height, since a smaller 105 proportion of any bank failure plane is affected by roots where there are shallow roots and high banks 106 (Abernethy & Rutherfurd 1998; Beechie et al. 2006; Eaton & Giles 2009; Pollen-Bankhead et al. 2013; 107 108 Konsoer et al. 2016). Consequently, river bank stability models do not recognize Davies et al.'s (2017) 109 proposed process of aggradational accumulation of short roots (Thomas & Pollen-Bankhead 2010; Pollen-Bankhead et al. 2013). Similarly, palaeosols from this period in Earth history do not support the 110 111 development of rapidly aggrading soils that build up thick rootleted horizons on the scale of channel 112 depths (Kenrick & Crane 1997; Retallack 1997; Algeo & Scheckler 2010; Mintz et al. 2010). Thus, it 113 appears unlikely that the binding effect of plants on floodplains was substantial. However, even if these 114 hypotheses are proven they would be allied to the unique set of circumstances recorded by Santos et al. (2017) that were ideal for the accumulation of fines. Consequently, any binding, trapping, and 115 production of fines by early land plants was likely only an additional component to this larger 116 117 tectonically and environmentally driven signal. Our analysis of root-depth evolution is claimed to be 'selective' and 'inaccurate', yet no evidence is provided to support this 'critique'. We assume that the 118 119 well understood and accepted increase in root depths intrinsic to our compiled dataset is not being challenged. Furthermore, our key point that root depths were very small in early land plants is directly 120 121 supported by Davies et al. (2017); these plants had "only limited root-like organs". So we are unclear 122 what aspect of our study is being challenged; rather the key point is strongly affirmed by these authors.

Regarding what Davies et al. (2017) consider as "numerous errors and contradictions" of our data on 123 palaeobotany, we make five points: (i) for obvious reasons we focus on plant fossils that have been 124 125 linked to the rise of meandering deposits, rather than on palynology of non-preserved environments, or 126 intramontane floras; (ii) our assertion that the earliest vegetation may have exerted similar influence to pre-existing microbial mats is claimed to be "unfounded" yet the only evidence offered is that these are 127 mechanically different; (iii) Wellman et al. (2013) show that early land plants spread from Gondwana; 128 (iv) we did not question vegetation cover by the Early Devonian, but rather its impact on sedimentation, 129 130 a different point; and (v) the megabias against Palaeozoic dryland plants discussed by Falcon-Lang et al. (2011) considers Pennsylvanian strata, not Ordovician-Devonian strata that are the subject of our 131 manuscript. Finally, the claim of Davies et al. (2017) that the widespread development of favourable 132 terrestrial environments would be expected to trigger a polyphyletic plant radiation is unfounded. We 133

134 contend that the difficult challenge for plants, of making the transition to terrestrial habitats, makes it135 unsurprising that it was only achieved once.

136

137 Conclusions

In their summary statement, Davies et al. (2017) argue that a "singular and unidirectional facies shift 138 139 occurs in the global rock record in close stratigraphic alliance with evolutionary developments in the 140 palaeobotanic record". However, we show that the meandering facies shift occurs multiple times and is 141 bidirectional. We also show herein that the correlation between the initial timing of this facies shift and palaeobotany does not imply causation. We argue that the limited size, root-depth and environmental 142 range of early plants were too small to influence river bank stability and to drive the change to 143 meandering. Furthermore, we argue for a two-phase process: firstly, tectonic and environmental 144 influences provided a unique set of conditions for the accumulation of large fines-rich low-gradient 145 coastal plains that provided optimal conditions for river bank stability, and thus the growth of 146 meandering channels. In turn, these aided plant terrestrialization by providing ideal environmental 147 conditions for land plant growth and subsequent evolution, leading to deeper root systems that provided 148 149 significant bank stability and led to a semi-permanence of this facies shift, with the exception of major mass extinctions. In support of these arguments, we provide an array of evidence for the presence of 150 abiotic meandering channels. In contrast, there remains no mechanistic evidence for the role of early 151 152 land plants in generating meandering planforms, and in fact, experimental, field, and numerical evidence all suggest that the braided-meandering transition is linked to much greater root depths, that 153 scale with channel depth. In summary, we maintain our argument that tectonic and environmental 154 conditions were key for the initial facies shift, and not early land plants, and that later plant evolution 155 156 reinforced this initial shift.

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