

# DEEP TIME BIOGEOMORPHOLOGY: THE CO-EVOLUTION OF LIFE AND SEDIMENTS

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Amongst all the disciplines in Earth Sciences, paleontology and sedimentary geology share a particularly striking and complicated frontier. On the one hand, some of the topics that they encompass are apparently separated by huge gulfs in methods and expertise: multiple degrees of separation need to be counted to get from, say, molecular phylogeny to sediment diagenesis, or paleophysiology to sequence stratigraphy. Yet there are arguably further areas where the boundary between the subjects is far more porous, consisting of sub-disciplines that refuse to be pigeon-holed and instead demand consensus between paleontologists and sedimentary geologists. This hazy border zone is the natural territory of PALAIOS, the remit of which is to emphasize “*the impact of life on Earth's history as recorded in the paleontological and sedimentological records*”, and which has previously published seminal advances in topics such as ichnology, taphonomy, and carbonate sedimentology. Recognizing this, this first of two thematic sets in the journal, which seek to explore how the sedimentary rock record has chronicled ancient life and sediment interactions, might seem unnecessary.

24 Yet what makes these collected papers distinct is that they defy classification within any  
25 particular sub-discipline: rather these are either ‘paleontological’ papers that pay additional  
26 attention to sedimentological context or ‘sedimentological’ papers that emphasise the  
27 importance of life in sedimentary environments. In each instance they demonstrate the  
28 potential to understand much more about ancient Earth when the procedures of the two  
29 disciplines are undertaken in unison, and hopefully showcase avenues of exploration to  
30 inspire further research in this vein.

31 The collected papers demonstrate the intrinsic links between fossils and the strata that host  
32 them, with a particular emphasis on siliciclastic strata where such linkages have traditionally  
33 and oftentimes been overlooked. Together they show how investigation of these connections  
34 can reveal high-definition records of feedback between organisms and their physical  
35 environments at the time of deposition and illustrate case studies of sedimentary-stratigraphic  
36 characteristics that developed in synchronicity with the evolving biosphere at Earth’s surface  
37 (see Davies et al., 2020). The papers are necessarily selective and cannot encompass the  
38 entirety of the diverse life-sediment interactions that have existed throughout geologic  
39 history, but they serve to highlight the types of observations that can be employed and the  
40 detailed interpretations that can be made from them. This first thematic set has a loose  
41 running theme of ‘plants’, documenting examples of vegetation-environment interactions  
42 recorded in the rock record from the Mississippian to the Pliocene, and the forthcoming  
43 thematic set will follow a similar path for ‘animals’. These two kingdoms dominate the  
44 macroscopic biosphere that defines the Phanerozoic and have stamped their mark on the rock  
45 record over the last half a billion years (though this is not to understate the importance of  
46 microbiota, which have had such a clear impact on the sedimentary record (e.g., Riding,  
47 2000) that they may warrant a similar thematic set in the future).

49 The timeliness of the thematic sets comes from recent developments in our understanding of  
50 modern and recent geomorphic processes. Under the adage that “the present is the key to the  
51 past”, modern sedimentary environments are routinely utilized as analogues to inform facies  
52 models for ancient sedimentary strata (e.g., James and Dalrymple, 2010). The epistemic link  
53 between the modern and the ancient is long accepted: observations of cause and effect in  
54 extant Earth surface processes are used to induct the laws of nature that themselves inform  
55 abductive explanations for sedimentary and paleobiological phenomena archived in the rock  
56 record (Kleinmans et al., 2010). However, the progress of different subjects shifts at different  
57 paces, and we suggest that recent advances in our understanding of modern environments,  
58 specifically from the sub-discipline of biogeomorphology (Viles, 1988), have yet to be fully  
59 realised into investigations of ancient life and environments.

60 Biogeomorphology is the umbrella term for geomorphological investigations that focus on  
61 the linkages between life and Earth surface processes and landforms, and is a field that has  
62 witnessed a considerable expansion in recent years, borne out by multiple contemporary  
63 reviews of the topic (e.g., Coombes, 2016; Phillips, 2016; Viles, 2020, 2022; Larsen et al.  
64 2021; Mason and Sanders, 2021; Rice, 2021). The general consensus in the geomorphic  
65 community is that focussed study of biogeomorphic phenomena have cumulatively  
66 demonstrated that geomorphic-ecologic interdependencies are fundamental in modern  
67 landscapes (Viles, 2020), and underlined the futility of attempting to fully understand  
68 “abiotic” Earth surface processes without reference to the organisms that interact with them.  
69 Such an integrated understanding appears to lag in studies of ancient environments. While the  
70 evolutionary significance of ancient biogenic materials and structures such as coal, reefs and  
71 coquinas have been noted (see Davies et al., 2020), in focussed case studies it has sometimes  
72 been considered just enough to proclaim the interpreted environmental facies of a fossil of  
73 interest (see Wright, 2019), or to explain sedimentary patterns with reference only to

74 tectonics or climate. Biogeomorphic research has underlined just how important life can be as  
75 a sedimentary-geomorphic agent and a host of seemingly esoteric interactions have ultimately  
76 been shown to be of major importance. Examples are too numerous and diverse to do justice  
77 with a simple list, but we now know how the activity of fish can help determine sediment  
78 mobility (Pledger et al., 2017), how caddisfly silk can have long-lasting impacts on bed  
79 hydraulics (Johnson et al., 2009), how the extent of earthworm bioturbation varies by climate  
80 zone (Paton et al., 1995), how the shape of coastlines can be wholly dependent on the life-  
81 history traits of the plants that colonize them (Schwarz et al., 2017), and how the interplay of  
82 predators, herbivores and riparian vegetation determines gross river morphology (Beschta  
83 and Ripple, 2012). If modern organisms are so essential to the operation of the landscapes  
84 and seascapes they occupy, it is wholly implausible that ancient organisms were passive  
85 inhabitants of their surroundings. Despite the optical illusion of museum dioramas, trilobites,  
86 lycopsids and dinosaurs did not just sit around in an unchanging trompe l'oeil of their  
87 background environment, they must have interacted and in some cases engineered the Earth  
88 surface processes around them. It must be admitted that ancient biogeomorphic phenomena  
89 recorded in the sedimentary-stratigraphic record may sometimes be underdetermined by  
90 available evidence (Davies et al., 2020), or definitively reveal only one part of a more  
91 complicated whole that remains open to reasoned interpretation. However, the papers  
92 collected here demonstrate that this is not always the case, and efforts to unravel  
93 paleobiological-sedimentological interdependencies have the potential to pay great dividends  
94 as we seek to understand how the Earth system has evolved over geologic time.

### 95 *The Importance of Temporal and Spatial Scales*

96 One aspect of recent biogeomorphological research that is especially pertinent to deep time  
97 investigations is the emerging recognition of the importance of temporal and spatial scale  
98 with respect to observations and phenomena (e.g., Post, 2019; Larsen et al., 2021; Phillips

99 2021). Larsen et al. (2021) consider that the intensity of known biogeomorphic feedbacks  
100 becomes more pronounced with decreasing spatial and temporal scale and have highlighted  
101 the limitation of understanding biogeomorphic feedback on greater than centennial scales,  
102 due to the finite historicity of instrumental records. Unconfined by such time limitations, the  
103 geologic perspective clearly has the potential to inform on the deep roots of modern  
104 biogeomorphic phenomena (e.g., Davies et al., 2021). Multiple studies have recognized the  
105 broad correlation between temporal and spatial scale in ecologic, geomorphologic,  
106 sedimentologic and biogeomorphic phenomena (Kleinhans et al., 2010; Miall, 2015; Post,  
107 2019; Davies et al., 2020; Davies and Shillito, 2021; Larsen et al., 2021) (Figure 1). The  
108 sedimentary-stratigraphic record is uniquely able to attack questions about the role of life in  
109 Earth surface processes because its longevity enables the record of such to be interrogated at  
110 different scales. At outcrop, this can be at the small spatio-temporal scale familiar from  
111 modern biogeomorphology, but the sedimentary-stratigraphic record also offers a perspective  
112 across the whole planet over geological timescales.

113 *Small scale records: biogeomorphic phenomena at outcrop*

114 Just because something happened a long time ago doesn't mean it took a long time to happen.  
115 There is increasing recognition that the stratigraphic timescales that are archived at outcrop-  
116 scale can be discretized to surprisingly short intervals (Paola et al., 2018; Holbrook and  
117 Miall, 2020; Davies and Shillito, 2021). Although the time taken to deposit a whole  
118 stratigraphic formation or basin fill can be very long, because sedimentary basins are large,  
119 because sedimentation is localized within such basins at any one time (Runkel et al., 2008;  
120 Bhattacharya et al., 2019; Davies et al., 2019), and because the sedimentary-geomorphic  
121 elements within them generate pockets of high accommodation space (e.g., between delta  
122 lobes: Ganti et al., 2020), the snippets of basin fill that are destined to appear as rock outcrops  
123 have a high potential to sample phenomena that occurred on familiar 'human' timescales.

124 This means that the perspective available from individual field investigations of outcrop can  
125 witness phenomena that are directly analogous in time-length scale to modern biogeomorphic  
126 features. The counterintuitive nature of such incidents has traditionally provoked a demand  
127 for special explanation: standing Carboniferous trees have been accounted for by rapid  
128 subsidence (Bailey, 2011) and apparently contemporaneous communities of burrows on  
129 shared substrates have been dismissed as implausible (McIlroy and Garton, 2010). Yet both  
130 these instances have been shown to be more readily explainable as mundane artefacts of the  
131 relationship between the time-length scales of ancient environments and present day outcrop  
132 (Miall, 2015; Holbrook and Miall, 2020; Allport et al., 2022). Fundamentally this means that  
133 they are not surprising or exceptional: rather, they are examples of what Paola et al. (2018)  
134 termed the "strange ordinariness of the stratigraphic record".

135 If we consider the sedimentary record at outcrop to be essentially ordinary, this opens a huge  
136 realm of possibility to understand ancient biogeomorphic interactions. If the record is  
137 archiving day-to-day processes, and we can recognise phenomena such as plant-animal-  
138 sediment interactions in Carboniferous estuaries (McMahon et al., 2022, this issue), woody  
139 debris accumulations in Paleozoic river systems (Trümper et al., 2022, this issue), or putative  
140 beaver dams in Pliocene strata (Davies et al., 2022, this issue), then we can be confident we  
141 are witnessing normal biogeomorphic processes that are directly analogous to modern  
142 occurrences. Through further investigation, the hope is that a multitude of similar instances  
143 can be recognised and the deep time historicity and origins of a plethora of modern-day  
144 processes can be better understood (e.g., Corenblit et al., 2015).

#### 145 *Large scale records: biogeomorphic trends from whole rock record analyses*

146 A vantage unique to studies of the sedimentary-stratigraphic record is that of the huge spatio-  
147 temporal scale, invisible to biogeomorphic investigations of modern environments. If global

148 compendia of supposed biologically-dependent or biologically-influenced lithologies,  
149 materials, sedimentary structures and facies can be compiled, multi-million year secular  
150 trends can be identified that reveal step-changes in the operation of Earth surface processes  
151 throughout the planet's evolution. Examples of research in this vein have already  
152 demonstrated secular change in biogenic sediments such as carbonates or coal (e.g., Riding,  
153 2006; Diessel, 2010), the influence of land plants on fluvial processes and landforms (e.g.,  
154 Davies and Gibling, 2010; McMahon and Davies, 2018) and the impact that bioturbation had  
155 on marine and continental environments (e.g., Mángano and Buatois, 2017; Buatois et al.,  
156 2022). Such observations contextualize smaller scale biogeomorphic phenomena seen today,  
157 as well as illuminating the evolutionary trajectory of the Earth system. Further focussed  
158 study on the small scale records of individual ancient successions has the long-term promise  
159 to produce more case studies, and unveil new aspects of comparison, that can further refine  
160 these large scale perspectives. For example, prominent blindspots exist in our knowledge of  
161 the ancient record, particularly with respect to poorly recorded organisms such as fungi. The  
162 work of Gibson (2022, this issue) provides an example showing how fungi-environment  
163 interactions may be identified and should act as a spur to gather further information in this  
164 field.

165 The short- and long-term perspectives offered by the rock record make it a powerful but  
166 presently underutilized tool for understanding how life makes surface processes on Earth  
167 unique amongst known planets. To do this successfully, understanding the scale of  
168 observations is essential, an issue underlined by Mays and McLoughlin (2022, this issue)  
169 who highlight how the short-term archive of wildfire reveals the global significance of this  
170 phenomena, while simultaneously ruling it out as a plausible sole explanation for long term  
171 trends in the sedimentary-stratigraphic record such as the Early Triassic 'coal gap' (Retallack  
172 et al., 1996). The perspective that the long-term geological record is in many ways a granular

173 patchwork of high-resolution short-term records presents a challenge to its interpretation, but  
174 a robust appreciation of this promises a far greater understanding of how the Earth system  
175 evolved. This further underlines the necessity of ever more case studies of life-sediment  
176 interactions in deep time. If ‘paleobiogeomorphology’ is to follow the successful trajectory of  
177 its modern counterpart, the first step is the accumulation of a multitude of specific examples  
178 which will together unravel the intrinsic importance of life to our planet. Etienne (2010) and  
179 Viles (2022) have argued that modern biogeomorphology has moved from ‘fun’ to  
180 ‘fundamental’ through the accrual of specific examples. If more work follows the papers  
181 collected here, the potential of the deep time record will be more fully realised, so long as the  
182 artificial border wall between sedimentology and paleontology continues to crumble.

### 183 PAPERS IN THIS THEMATIC SET

184 The papers in this first thematic set approximately follow the theme of ‘plants’, but inevitably  
185 other organisms also reveal their importance. **McMahon et al.** (2022, this issue) consider the  
186 sedimentary structures that are produced by different organisms, and demonstrate how, by the  
187 middle of the Palaeozoic, both plants and animals were affecting the array of phenomena  
188 archived in estuarine siliciclastic facies. With a high resolution case study from the west of  
189 Ireland, they detail some of these features and show how their distribution was controlled by  
190 their position relative to the ancient tidal prism, with plants dominating the biogenically  
191 induced/influenced features of landward facies, and animals supplanting vegetation as the  
192 dominant biogenic influence in basinward facies toward the estuary mouth.

193 As plants continued to colonize the interior drylands of continents throughout the late  
194 Palaeozoic, large woody debris became an increasingly important component of epiclastic  
195 systems and strata. Significantly, as arborescent gymnosperms evolved and diversified,  
196 woody plant biomass induced changes in the environments of erosion, transport and



197 deposition of continental sedimentary systems. **Trümper et al.** (2022, this issue) provide  
198 further insights into the taphonomy and geo-engineering potential of woody debris via a  
199 detailed record of large silicified trunks that characterize Middle Pennsylvanian–early  
200 Permian strata of east-central Europe. They demonstrate how climatic seasonality in the late  
201 Palaeozoic subtropics and plant biodiversity partitioning at the local topographic scale  
202 encouraged the spread of woody gymnosperms, but that the climatic and tectonic settings of  
203 this time also favoured their preservation, offering a unique window into the plant-sediment  
204 interactions from this time.

205 The order of magnitude increase in biomass associated with the novel vegetation discussed  
206 by McMahon et al. (2022, this issue) and Trümper et al. (2022, this issue) also opened the  
207 door to new surface-atmospheric processes that permanently altered the sedimentary-  
208 stratigraphic record. Chief among these was the introduction of significant quantities of  
209 combustible fuel, in the form of woody material. When coupled with the increase in  
210 atmospheric oxygen – itself driven by the oxygenic photosynthesis of land plants – fire, for  
211 the first time, became a significant shaper of landscapes, ecosystems, evolution and  
212 sediments. **Mays et al.** (2022, this issue) explore such feedbacks between flora and wildfires  
213 in the context of the Permian-Triassic Boundary Event. They illustrate how wildfires likely  
214 played a role even in ever-wet settings at the time, and may in part have exacerbated  
215 extinctions.

216 Plants are macroscopic, complex, tissue- and organ-grade multicellular organisms. Another  
217 clade of complex multicellular eukaryotes, the fungi, are frequently associated with  
218 vegetation and are also intimately linked with Earth’s lithospheric and biospheric processes  
219 via the decay and breakdown of plant biomass, binding of soils, and through the acidic  
220 bioweathering of minerals and rocks. Despite the increasing awareness of how plants and  
221 animals have shaped the sedimentary-stratigraphic record, disentangling the influence of

222 fungi has been hampered by their woefully understudied fossil record. **Gibson** (2022, this  
223 issue) studies the rare fungal content of Zechstein palynological preparations, which provides  
224 new insight into the composition of the Zechstein forest understory, and its influence on the  
225 environment during the Permian Period.

226 Plant-animal interactions are also important drivers of biogeomorphic processes, and through  
227 these certain animals can have an outsized effect on entire landscapes. A fundamental tenet of  
228 modern ecology is that the behaviour of certain animal species can exert an inflated impact  
229 on the structure of entire ecosystems. **Davies et al.** (2022, this issue) consider the  
230 sedimentological impacts of one such ecosystem engineering animal that is celebrated in  
231 modern environments: the beaver. Using original field data from Pliocene strata of Arctic  
232 Canada, they construct a facies model that sheds light on how the evolution of putative  
233 beaver dams and other, passive, woody accumulations changed fluvial sedimentary signatures  
234 and habitats, and also influenced the environment occupied by other warm Arctic flora and  
235 fauna.

236 Cumulatively, these five papers provide snapshots of ancient life-environment interactions  
237 from across a c.350 million year period and demonstrate just how innate life has been in  
238 sculpting both landscapes and the sedimentary record. They merely scratch the surface of  
239 what may be achievable with focussed research in this area, but illustrate a fact of critical  
240 importance: many seemingly ‘abiotic’ features familiar in the modern world simply would  
241 not exist, or be different, had life never evolved on planet Earth.

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367

#### 368 **FIGURE CAPTION**

369 FIGURE 1 – Diagram showing examples of the relationship of approximate time and length

370 scale in different phenomena. Length scale modified from Larsen et al. (2021) to refer to

371 organism-related length scales. Green boxes indicate time-length scales of biological

372 processes and dashed green line refers to dynamic time-length scales within the lifespan of an

373 individual organism. Yellow rounded boxes illustrate a selection of bio-sedimentary

374 phenomena (see Davies et al., 2020 for further examples). Purple ovals refer to hierarchical

375 elements of the sedimentary record, from individual bedforms through depositional elements

376 (e.g., channels, delta lobes), to depositional cycles and basins. Blue dotted lines show

377 approximate scales of geological samples from individual rock outcrops through whole

378 stratigraphic formations to entire basin fills. Grey shaded areas show the extent of

379 biogeomorphic evidence confidently attainable from modern studies (Larsen et al., 2021).

380 Significantly, geological samples can potentially archive any of the phenomena that occur at

381 a smaller time-length scale, rendering the sedimentary stratigraphic record particularly suited



382 to identifying small scale phenomena at outcrop and large scale phenomena from holistic  
383 analysis – some of which cannot be accessed through modern biogeomorphic investigation.  
384 From a biogeomorphic perspective there is multidirectional feedback between higher and  
385 lower order phenomena that are contemporaneous: e.g., from small to large scale, community  
386 succession can influence channel planform which in turn influences basin fill; from large to  
387 small scale, the nature of depositional elements can influence the habitats of individual  
388 lifeforms that may be more or less predisposed to burrow. The diagram has been modified  
389 from components of the following figures, which the reader is recommended to consult for  
390 further details: Kleinhans et al. (2010, Fig. 2); Miall (2016, Fig. 11); Post (2019, Fig. 3.1);  
391 Davies et al. (2020, Fig. 2); Davies and Shillito (2021, Figs. 25 and 26); Larsen et al. (2021;  
392 Fig. 1).

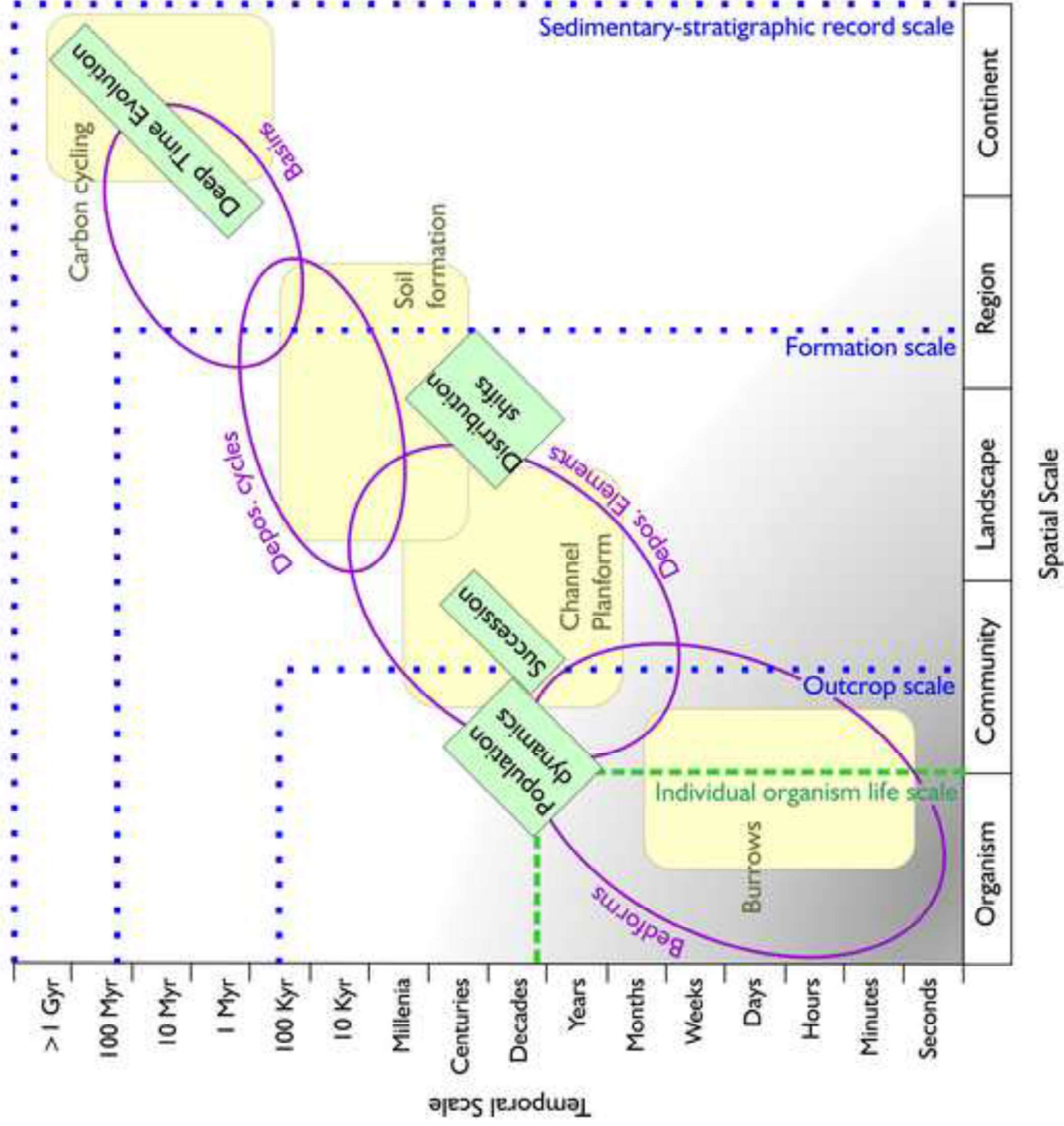


Figure 1