

1 **Considering river structure and stability in the light of evolution: feedbacks**
2 **between riparian vegetation and hydrogeomorphology**

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23 **Abstract**

24

25 River ecological functioning can be conceptualized according to a four-dimensional
26 framework, based on the responses of aquatic and riparian communities to
27 hydrogeomorphic constraints along the longitudinal, transverse, vertical and temporal
28 dimensions of rivers. Contemporary riparian vegetation responds to river dynamics at
29 ecological timescales, but riparian vegetation, in one form or another, has existed on
30 Earth since at least the Middle Ordovician (c. 450 Ma) and has been a significant
31 controlling factor on river geomorphology since the late Silurian (c. 420 Ma). On such
32 evolutionary timescales, plant adaptations to the fluvial environment and the subsequent
33 effects of these adaptations on aspects of fluvial sediment and landform dynamics
34 resulted in the emergence, from the Silurian to the Carboniferous, of a variety of
35 contrasted fluvial biogeomorphic types where water flow, morphodynamics and
36 vegetation interacted to different degrees. Here we identify several of these types and
37 describe the consequences for biogeomorphic structure and stability (i.e. resistance and
38 resilience), along the four river dimensions, of feedbacks between riparian plants and
39 hydrogeomorphic processes on contrasting ecological and evolutionary timescales.

40

41 **KEYWORDS:** *fluvial biogeomorphic succession; riparian vegetation; functional traits;*
42 *vegetation evolution; scale-dependant feedback; ecosystem engineer; ecosystem*
43 *resistance and resilience; niche construction*

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45

46 **Introduction**

47

48 Riparian ecosystems, developing at the interface between water and land, are among
49 the most geomorphologically dynamic and variable environments on the Earth surface in
50 terms of (i) structure, function and diversity (Naiman and Décamps, 1997) and (ii)
51 strength of abiotic-biotic feedbacks (Corenblit *et al.*, 2007). The biogeomorphic structure
52 and stability of riparian ecosystems are the products of a long and complex history, in
53 which a hierarchy of abiotic-biotic feedbacks developed over hundreds of millions of
54 years.

55 From a hydrogeomorphic perspective, geomorphologists have long proposed
56 frameworks describing fluvial geomorphic adjustments from the scale of the hydrological
57 basin (Schumm, 1977) to the scale of the river channel (Leopold and Maddock, 1953;
58 Wolman, 1955) (see also Church, 2002). Based on these geomorphic frameworks,
59 hydroecologists have conceptualized river ecological functioning in four dimensions:
60 longitudinal, transverse, vertical and temporal. This four-dimensional framework was set
61 out by Amoros *et al.* (1987a) (concept of 'fluvial hydrosystems') and Ward (1989).

62 The four-dimensional framework provides a strong conceptual basis for studying river
63 ecosystem-level functioning on the basis of matter and energy fluxes. Specific
64 conceptual models related to this framework include the river continuum (Vannote *et al.*,
65 1980), nutrient spiraling (Newbold *et al.*, 1982), flood pulse (Junk *et al.*, 1989), patch
66 dynamics (Townsend, 1989), boundary-interface (Naiman and Décamps, 1997), natural
67 flow regime (Poff *et al.*, 1997), flow pulse (Tockner *et al.*, 2000), and river discontinuum

68 (Poole, 2002). These models postulated that aquatic and riparian community structure
69 could be explained by considering the linkage between the life-history traits of species
70 and the spatiotemporal patterns of hydrogeomorphologic processes along the different
71 dimensions (Townsend and Hildrew, 1994). Many studies undertaken within this
72 framework have outlined the huge diversity of aquatic and riparian communities linked to
73 spatial heterogeneity in hydrogeomorphic parameters and to temporal variability along
74 the river dimensions (Pickett and White, 1985; Poff *et al.*, 1997; Ward *et al.*, 1999;
75 Latterell *et al.*, 2006; Thorp *et al.*, 2006; Bornette *et al.*, 2008).

76 However, these models were based on a physical habitat template (*sensu*
77 Southwood, 1977) that focused strictly on how hydrogeomorphic heterogeneity and
78 variability affected the biotic compartments. They did not consider explicitly how and to
79 what extent river spatial dimensions adjust at nested spatiotemporal scales under the
80 control of engineer (*sensu* Jones *et al.*, 1994) plant species which exert profound effects
81 on hydrogeomorphic processes, river geomorphology and habitat conditions. Thus, as
82 suggested by Fisher *et al.* (2007) and Wainwright *et al.* (2011), they overlook, at least to
83 a certain extent, certain aspects of the highly significant role of abiotic-biotic feedbacks
84 linked to aquatic and riparian plant species within river ecological functioning.

85 Within river corridors, riparian vegetation controls or modulates the patterns of ground
86 and surface water (Tabacchi *et al.*, 2000), fine sediment (Gurnell and Petts, 2006),
87 organic matter, nutrient (Francis *et al.*, 2009) and diaspore (O'Hare *et al.*, 2012) fluxes.
88 By modulating matter and energy fluxes, riparian plants cause drastic modulation of
89 fluvial landform dynamics (Gurnell *et al.*, 2012; Gurnell, 2014). They also modify the
90 biophysicochemical properties of riparian substrates by means of roots, their

91 interactions with bacteria (Doty *et al.*, 2005) and mycorrhizal fungi (Beauchamp *et al.*,
92 2006), uptake of nutrients (Pinay *et al.*, 2000) and their release of organic matter and
93 exudates in the substrate. Furthermore, they strongly modulate local microclimatic
94 conditions, such as air and ground surface temperature and humidity, and light regime
95 (for a review see Tabacchi *et al.*, 2000).

96 The aim of this paper is to explore the role of engineer plants in modulating the four
97 dimensions of river systems, and the abiotic and biotic interactions that result from these
98 modulations. We stress that the four-dimensional framework needs to be reinforced by
99 considering feedbacks between vegetation and hydrogeomorphic dynamics on both
100 ecological ($<10^3$ year) and evolutionary ($>10^5$ year) timescales in order to obtain a better
101 understanding of two fundamental properties of riparian ecosystems linked to system
102 stability: resistance and resilience (Holling 1973, 1996; O'Neill *et al.*, 1986; Tilman,
103 1996).

104 We document, according to palaeontological and geological evidence: (i) the
105 fundamental developmental phases of river ecosystems from the beginning of the
106 colonization of continents by land plants (in the Middle Ordovician), (ii) the pattern of
107 abiotic-biotic feedbacks related to each developmental phase on an evolutionary time
108 scale, and (iii) the resultant effects on river biogeomorphic structure, resistance and
109 resilience along the four dimensions. Based on the literature and on empirical
110 contemporary data collected on the River Tech (Pyrenees, France), we propose an
111 original explanation of how the hierarchy of abiotic-biotic feedbacks may have led to the
112 emergence of characteristic fluvial biogeomorphic types (FBT) which we define here and
113 that represent specific conditions of biogeomorphic resistance and resilience ability,

114 dominant ecological strategies and diversity. We then examine the FBTs in the
115 successional framework first proposed by Corenblit *et al.* (2007), i.e. the fluvial
116 biogeomorphic succession model (FBS).

117

118 **The fluvial biogeomorphic succession model**

119

120 Corenblit and Steiger (2009) stressed that the overall evolution of riparian vegetation
121 morphological, physiological and phenological functional traits favouring their resistance
122 to hydraulic constraints, sediment scouring and burial and their resilience after floods
123 may have led to major ecosystemic modifications in rivers. In addition to affecting fluvial
124 geomorphology plant functional traits affected riparian ecosystem resistance and
125 resilience and resulting structure, along the biologically constructed longitudinal,
126 transverse and vertical river dimensions. The authors proposed the fluvial
127 biogeomorphic succession model to describe the structural and functional
128 consequences of abiotic-biotic feedbacks on the riparian ecosystem (Corenblit *et al.*,
129 2007) (Fig. 1). The FBS is related to a recurrent and characteristic positive feedback of
130 matter aggregation, stabilization and vegetation growth and succession, during which
131 the riparian ecosystem shifts from a highly resilient state dominated by extrinsic
132 hydrogeomorphic processes and r-strategist organisms to a resistant state dominated
133 by intrinsic biological processes and K-strategist organisms (Corenblit *et al.*, 2009a;
134 Francis *et al.*, 2009). Many studies highlighted the way the positive feedback is driven
135 by pioneer engineer riparian trees (e.g. in the temperate climate, species of *Populus*,

136 *Salix*, *Alnus* and *Tamarix* genera) that trap sediment, organic matter, nutrients and
137 diaspores within active river channels (for a review see Gurnell, 2014).

138 The FBS model was initially defined with empirical data from the River Tech (for a full
139 description see Corenblit *et al.*, 2007; Corenblit *et al.*, 2009a,b). Figure 2 schematises
140 the biogeomorphic structure and sediment dynamics along the transverse and vertical
141 gradients of hydrogeomorphic connectivity and vegetation succession, as observed
142 within the river's piedmont zone. Feedbacks between vegetation succession and the
143 construction of fluvial landforms led to a reciprocal dependency between the physical
144 environment and the floristic composition which was documented using a Canonical
145 Correspondence Analysis (Fig. 3). Correlations between the hydrogeomorphic variables
146 and the floristic composition reported in Table 1 suggest that vegetation succession on
147 the River Tech follows a lateral gradient of hydrogeomorphic disconnection and a
148 vertical (topographic) gradient of sediment grain-size fining upwards related to sediment
149 trapping by engineer plants.

150 Based on observations from the palaeontological and sedimentary rock records,
151 Davies and Gibling (2013, their Fig. 25) showed that it may be possible to conceptually
152 apply the FBS, initially proposed at an ecological timescale, to an evolutionary
153 timescale. This requires describing the hierarchy of feedbacks between vegetation
154 evolution and fluvial geomorphic adjustments that would have existed at different
155 intervals of the Palaeozoic Era. Such a description suggests that the ways
156 contemporary riparian ecosystems organize along the four river dimensions can be
157 placed within an eco-evolutionary history (*sensu* Post and Palkovaks, 2009) by
158 considering (i) how ancient plants responded to hydrogeomorphology, (ii) how these

159 responses fed back on hydrogeomorphic processes and fluvial landforms, and (iii) how
160 the modified fluvial geomorphologic framework fed back on the evolutionary adaptations
161 of vegetation and on ecosystem structure, function and stability.

162

163 **Changing biogeomorphic feedbacks along the river dimensions on an**
164 **evolutionary timescale**

165

166 Plants have colonized non-marine environments since at least the Middle Ordovician (c.
167 470-458 Ma). They evolved traits that improved their ability to face terrestrial constraints
168 and more specifically to colonize different patches of the riparian environment, including
169 diverse adaptations that increased their resistance to long periods of aqueous
170 submersion or water deficit, intermittent burial by sediment and mechanical constraints
171 imposed by flowing water (for a review see Bornette *et al.*, 2008). Aided by these
172 adaptations, land plants greatly diversified between the Silurian and the Carboniferous
173 (Niklas *et al.*, 1983) and spread within river corridors from downstream to upstream
174 habitats and from river margins to perched floodplains and river channels, and,
175 ultimately, to upland environments. As riparian plants progressively colonized entire
176 river corridors, they increased their propensity to frequently and permanently modulate
177 hydrogeomorphic processes, thus contributing to a wholesale global re-shaping of fluvial
178 landscapes (Gibling and Davies, 2012). These modulations of hydrogeomorphic
179 processes and fluvial landforms have occurred in all four dimensions of river systems: (i)
180 the longitudinal dimension, related to the upstream-downstream gradient of energy from
181 headwaters to the river mouth; (ii) the transverse dimension, related to the gradient of

182 hydrological connectivity (in terms of the duration and frequency of plant submersion)
183 and depending on the distance to the floodplain of a water channel; (iii) the vertical
184 dimension, related to exchanges between groundwater and surface flows and
185 depending on elevation above the water surface at low flow stage; and, (iv) the temporal
186 dimension, which considers state changes to the three spatial dimensions over time
187 (Fig. 4). The upstream-downstream gradient of energy needs to be considered here as
188 a conceptual simplification of the longitudinal variation in stream power.

189 Based on a synthesis of field evidence, Davies and Gibling (2010a,b, 2011, 2013)
190 drew on ancient geomorphic elements interpreted from the structures and internal
191 architecture of sedimentary strata to show how and to what extent fluvial landscapes
192 adjusted during the c. 242 Ma interval from the start of the Cambrian to the end of the
193 Carboniferous, with an apparent relationship between these changes and stepwise
194 evolutionary adaptations in early terrestrial vegetation (Fig. 5 and 6). The authors noted
195 that fluvial types greatly diversified over hundreds of millions of years, particularly
196 between the late Silurian and Pennsylvanian, ultimately leading to the appearance of
197 new *biogeomorphic types* (e.g. meandering, island braided, anastomosing; Fig. 6), with
198 niche-partitioned riparian ecosystems.

199 Despite the incompleteness and inherent bias of the geological record, which
200 preserves preferentially the alluvium of downstream reaches of lowland rivers, a number
201 of first appearances of biogeomorphic factors can be identified in the deep-time record.
202 The following sections outline the ongoing development of rivers as Palaeozoic plants
203 colonized the land, with the essential caveat that the apparent first appearances can
204 only be considered the latest possible appearances, and that the factors may have been

205 in operation even longer (though evidence for them may not be preserved, or not yet
206 discovered, in the palaeontological record).

207

208 *Before the Middle Ordovician: fluvial dynamics driven solely by physical processes*

209

210 Land plants (embryophytes) have colonized non-marine environments since at least the
211 Middle Ordovician (Taylor and Strother, 2008; Kenrick *et al.*, 2012). Prior to the
212 evolution of a terrestrial flora, fluvial landforms adjusted only to geological, geomorphic
213 and hydrological influences, with some potential analogy to ancient fluvial landforms
214 imaged on extraterrestrial bodies such as Mars (Grotzinger *et al.*, 2011). Geomorphic
215 adjustments were controlled by the interaction of factors associated with landscape
216 roughness, cohesiveness, surface slope and discharge. Landscape roughness and
217 cohesiveness are defined by factors such as bedrock properties, sediment grain size,
218 topography, and local factors that include cohesive permafrost or clays, whereas
219 surface slope factors govern the hydraulic geometry of the channel and its discharge. In
220 its broadest sense, the balance between these factors remains the single most
221 fundamental control on fluvial planform (Lazarus and Constantine, 2013). However, the
222 ubiquitous presence of vegetation in contemporary rivers has so significantly and
223 pervasively amplified the contributing factors to landscape roughness and cohesion that
224 modern fluvial systems are not comparable with the truly vegetation-free systems that
225 operated prior to the Middle Ordovician.

226 Schumm (1968) and Cotter (1978) were the first to suggest that braided rivers would
227 have dominated fluvial types prior to the greening of continents by plants. Fuller (1985)

228 and Miall (1996) also suspected that river channel patterns have adjusted their
229 morphology and dynamics over geological time in relation to the evolution of plants.
230 Further research suggests that, prior to the Silurian, only the *geomorphic phase* existed.
231 Rivers were broadly dominated all along the longitudinal dimension by bedload transport
232 between unconsolidated banks, and by wide and shallow channels with low topographic
233 relief at the channel margins; permanent muddy floodplains were probably lacking
234 (Gibling and Davies, 2012). Rivers from this time were fundamentally unstable and
235 probably widened rapidly and increased the number of internal braided channels during
236 individual precipitation events. Sheet-braided fluvial types thus widely dominated river
237 landscapes during this period, likely from piedmont zones to the coast and across all
238 climatic and latitudinal zones (Davies *et al.*, 2011; Long, 2011) (Fig. 5a and 6).
239 Sedimentological evidence shows that alluvial-fan deposits from the Cambro-Ordovician
240 incorporate only low quantities of muddy sediments, suggesting that weathering
241 processes were weak within river basins due to the absence of plants (Went, 2005).

242

243 *Silurian: first generations of plant adaptations to terrestrial and fluvial conditions*

244

245 During the late Ordovician and early Silurian, primitive small and poorly anchored land
246 plants, adapting to terrestrial conditions for the first time in Earth history, may not have
247 significantly affected hydrogeomorphic processes (i.e. water flow and coarse sediment
248 transport), beyond increasing local micro-landscape roughness and beginning to
249 promote the retention of fine-grained sediment in continental environments (Davies and
250 Gibling, 2010). However, this *pioneer phase* of the terrestrialization process remains

251 fundamental because the adaptive responses of land plants to subaerial conditions and
252 to the fluvial environment permitted them to spread efficiently from coastal zones along
253 the longitudinal and transverse dimensions of river corridors, affecting hydrogeomorphic
254 processes as the reach of their habitats advanced into the continental interiors (Fig. 5b).

255 Before this greening of the continents, microbial life, and probably lichens, were
256 already contributing to the formation of primitive soils enriched with Fe and P (Raven,
257 1995; Taylor *et al.*, 1995). They may also have stabilized surfaces sufficiently for
258 biochemical weathering to be enhanced (Dott, 2003; Kennedy *et al.*, 2006). As pointed
259 out by Phillips (2009) and Viles (2012), rock weathering by micro-organism is a
260 precursor of sediment removal. Phillips (2009) suggested that the energy necessary to
261 sustain rock weathering far exceeds the one required for sediment erosion and
262 transport. Thus, the Silurian represents a fundamental geological period where the
263 biosphere could begin storing and using energy for performing geomorphic work on
264 continental surfaces. This energy then was also transferred through trophic networks
265 permitting geomorphic work to be accomplished by different taxa and in different ways
266 (Naylor *et al.*, 2002).

267 The processes leading to soil formation would have been crucial for the colonization
268 of the continents by the first land plants. Land plants needed to develop specific
269 anatomical structures for transporting water and nutrients from the substrate to their
270 above-ground parts, overcoming desiccation and mechanical constraints imposed by
271 gravity, and reproducing out of water (Niklas, 1997; Kenrick and Crane, 1997; Willis and
272 McElwain, 2002; Gensel, 2008). Resulting adaptations included the development of
273 mechanical supports and rhizomes (Niklas, 1997). Coastal and fluvial environments are

274 ecologically disturbed and become frequently immersed and submerged. These
275 restrictive environments, with strong selection pressures, were almost certainly first
276 colonized by small, fast-growing plants, probably originating from green algae (Lewis
277 and McCourt, 2004), and which probably had high mutation rates. Because non-marine
278 environments were unoccupied, the fitness landscape of the first land plants was mainly
279 defined by physical and chemical factors (Niklas, 1997). From the end of the Ordovician
280 to the middle-Silurian small vascular tracheophyte genera, such as *Cooksonia*, *Rhynia*,
281 *Baragwanathia* and *Zosterophyllum*, diversified and colonized coastal zones as well as
282 lake and river margins (Greb *et al.*, 2006). Plants of bryophyte grade probably played a
283 significant role in rock weathering during this period (Lenton *et al.*, 2012).

284 Even though pioneer land plants from this interval were small and poorly anchored
285 embryophytes (Gensel and Andrews, 1978), and thus probably did not contribute to
286 controlling coarse bedload transport, these first land colonizers, especially those of
287 tracheophyte grade with vascular tissue, started to modify river geomorphology along
288 channels at the river mouth. The retention of muddy sediments within those vegetation
289 patches probably permitted the first generations of small tidally-influenced meandering
290 side-channels confined by muddy banks in the downstream reaches of lowland rivers
291 (Fig. 5b).

292 During the Late Silurian, vascular plants with more efficient supporting structures
293 continued to develop and silt and clay became prominent on basin-margin alluvial fans
294 and in alluvial deposits along the coastal zone. Probable rooting structures are known
295 from many Early Devonian localities and may also be present in Late Silurian strata
296 (Hillier, 2008; Kennedy *et al.*, 2012). Plants promoted the leaching of nutrients and

297 eutrophication of rivers (Lenton *et al.*, 2001). Such enhancement in nutrient availability
298 in river corridors may have caused an upstream-downstream eutrophication gradient
299 during the Silurian, increasingly promoting phytoplankton blooms, carbon and nitrogen
300 fluxes and anoxia from upstream to downstream within lowland plains, as Algeo *et al.*
301 (1995) and Algeo and Scheckler (1998) documented based on the Devonian marine
302 record. In relation to the production of mud through the interaction between vegetation
303 and the substrate, muddy floodplains started to develop in lowland plains during the late
304 Silurian. At the same time channeled-braided rivers (comprising more moderated,
305 narrow and stable braided channel features akin to those seen in modern braided
306 streams) started replacing the increasingly rare sheet-braided type in lowland plains
307 (Davies *et al.*, 2011) (Fig. 5c and 6). Vegetation cover increased dramatically in the
308 latest Silurian, paving the way for the early Devonian appearance of the first riparian
309 woody vegetation (Gerrienne *et al.*, 2011). At the close of this period, rivers with single-
310 thread meandering trunk channels, stabilized in part by the increasing number of
311 cohesive muddy floodplains and perhaps locally by organic structures, started to
312 develop (Davies and Gibling, 2010b).

313

314 *Devonian: strong abiotic-biotic feedbacks*

315

316 During the Devonian, the evolution of wood and riparian forests drastically changed river
317 landscapes through increased bank cohesion, surface roughness, and fine-grained
318 sediment supply. Vegetation diversified greatly and evolved toward lignified shrub, bush
319 and arborescent morphologies (Driese *et al.*, 1997; Elick *et al.*, 1998; Driese *et al.*, 2000;

320 Meyer-Berthaud *et al.*, 2010; Meyer-Berthaud and Decombeix, 2012; Stein *et al.*, 2012).
321 Storage of plant organic matter in soil increased during this period because of the
322 development of aerial and underground vegetation biomass and the appearance of
323 lignin resistant to decomposition (Gensel *et al.*, 2001). Lignin-bearing plants that
324 colonized lowland wetlands, such as *Lepidodendron* (Taylor and Taylor, 1993) and the
325 progymnosperm *Archaeopteris* (Meyer-Berthaud *et al.*, 1999), developed morphological
326 and physiological traits that increased their resistance to long-term submersion, turbidity
327 and fine-sediment burial (e.g. arborescence, adventitious roots, tolerance to anoxia).
328 Many types of rooting system developed during this period, some of them well ramified
329 and attaining more than 1m depth. The deep rooting system of plants such as
330 *Archaeopteris* (probably >4m) would have also favoured their propagation on floodplains
331 beyond the immediate river margins during the Devonian (Algeo and Scheckler, 1998).

332 By the Middle to Late Devonian, lowland plains were covered by dense riparian
333 forests in river corridors with different strata and dominated by tall trees with different
334 kinds of large and deep rooting (Bockelie, 1994). The Gilboa riparian forest documented
335 by Stein *et al.* (2007, 2012) represents a famous example encompassing an overstory
336 stratum dominated by the progymnosperm *Archaeopteris* and an understory stratum
337 dominated by the fern-like *Rhacophyton*. Such diversification of plant physiognomy can
338 be related to the fact that taller plants obtain better access to light and to wind for spore
339 dispersion (Niklas, 1997). Large size and morphologies of lycopods, arborescent
340 horsetails, progymnosperms and seed ferns thus provided an optimization of light
341 interception, mechanical support and spore dispersal and production (Niklas, 1997).
342 However, such attributes provide a selective advantage mostly in a stable environment.

343 Thus, such traits could possibly develop through a fundamental moderating feedback
344 between plant engineering and fluvial geomorphology, seemingly common during the
345 Devonian (Gibling and Davies, 2012).

346 The increase in the mechanical and physiological resistance of vegetation to
347 prolonged submersion or water-deficit stress led during this *biogeomorphic phase* to
348 drastic geomorphic changes in river systems through the concomitant stabilization of
349 river channels and the construction of floodplains. Tree roots greatly contributed to
350 stabilization of river banks and concentration of flow within a single channel with a
351 decreased width/depth ratio. Aerial structures increased surface roughness at the river
352 margin and on the floodplain, leading to fine-sediment retention and raised floodplains.
353 Rooted plants colonized laterally-accreting alluvial point bars and banks, contributing to
354 their stabilization and promoting at the same time fine-sediment trapping and retention
355 in specific locations within rivers' active tracts (Davies and Gibling, 2010b). As
356 suggested by Braudrick *et al.* (2009), a self-sustaining free meandering style only exists
357 in conditions where the bank strength is greater than that of deposited bedload and
358 where large amounts of fine suspended sediment can be deposited and preserved on
359 the migrating point bar. Devonian vegetation thus promoted the development of
360 meandering rivers (Fig. 5c,d and 6) dominated by lateral accretion, systematic lateral
361 channel migration, and chute and neck cutoffs (Cotter, 1978; Davies and Gibling,
362 2010b).

363 In part due to these biogeomorphic feedbacks between vegetation evolution and
364 geomorphology, by the Middle Devonian riparian ecosystems began to be partitioned
365 along the longitudinal, transverse and vertical dimensions. Such floristic contrasts were

366 a response to the diversification of conditions for submersion frequency and duration,
367 sediment erosion/deposition and nutrient availability (Allen and Gastaldo, 2006). This
368 floristic and geomorphic partitioning certainly involved a strong feedback between
369 engineer plants affecting water flow, sedimentation and landforms and their evolutionary
370 trajectory. This eco-evolutionary feedback was enhanced through the construction of
371 muddy and aggraded floodplains and may have promoted the evolution of certain plant
372 species, such as *Archaeopteris*, toward better competitive capacities and tolerance to
373 drier conditions and seasonality (Meyer-Berthaud *et al.*, 1999; Stein *et al.*, 2007, 2012).
374 The development of the arborescent physiognomy and resultant large canopies also
375 would have reinforced ecological partitioning through changes in soil habitat
376 (pedogenesis) and surface conditions (control of light intensity, humidity and
377 temperature). As illustrated by the Gilboa forest (Stein *et al.*, 2007, 2012), the new
378 Middle Devonian ecological niches led to a great increase in floristic and faunal
379 biodiversity and ecological strategies, linked to complex feedbacks between biotic and
380 abiotic processes (Gibling and Davies, 2012). Some Devonian plants may have been
381 capable of colonizing upland areas (Decombeix *et al.*, 2011).

382

383 *Carboniferous: culmination of complex non-marine ecosystems*

384

385 During the Carboniferous rivers attained the *ecological phase*. Muddy aggraded
386 floodplains were well developed and complex riparian ecosystems encompassing a
387 diverse array of plants and faunal species already existed (Willis and McElwain, 2002;
388 Greb *et al.*, 2006). Biotic interactions such as competition may have become preeminent

389 selection pressures defining the structure and function of the riparian ecosystem at the
390 scale of the entire river corridor within lowland plains and piedmont zones (Fig. 5d).

391 At the end of the Devonian and through the Carboniferous, a major turn-over and
392 diversification of riparian vegetation took place. By this time, the main vegetational traits
393 of response to hydrogeomorphology and influence on hydrogeomorphic conditions
394 already existed. Tall trees such as *Calamites* and *Psaronius* developed (Willis and
395 McElwain, 2002). Riparian plants continued adapting to water stress, and certain
396 species colonized drier raised levees within the alluvial plain (Falcon-Lang and Galtier,
397 2010). At the end of the Mississippian, gymnosperms developed deep rooting systems
398 at least 4m below the surface and colonized the driest, well drained areas of the alluvial
399 plains (DiMichele *et al.*, 2010). Most contemporary types of rooting had evolved by the
400 end of the Carboniferous (Pfefferkorn and Fuchs, 1991) and, of particular importance,
401 was the evolution of root systems that promoted high shear strength and resistance to
402 erosion (DiMichele *et al.*, 2010). The development of the seed habit also permitted trees
403 to colonize drier levees and expand into upstream valleys (Algeo and Scheckler, 1998)
404 and, in very dry lowland areas, even into coastal sabkhas (Falcon-Lang *et al.*, 2011b).
405 Wetland vegetation reorganized during the Moscovian-Kasimovian transition according
406 to a global increase of aridity. Wetlands were fragmented and further partitioned, and
407 riparian plants adapted further to drier and seasonal conditions (DiMichele *et al.*, 2009).
408 Woody cordaitales and conifers dominated drier Carboniferous episodes, forming dense
409 forested patches in inland settings (Falcon-Lang *et al.*, 2011a).

410 Another important adaptation during the Pennsylvanian was the ability of certain
411 plants to resist more efficiently mechanical constraints imposed by water flow during

412 floods and thus to grow directly within river channels (Fielding and Alexander, 2001;
413 Fielding *et al.*, 2009). Biomechanical traits promoting this habit include a high resistance
414 to breakage and flexibility of roots and aerial structures that permitted plants to modulate
415 the geomorphic setting in the most active zones of the river corridor. For example,
416 calamitalean sphenopsids were adapted to hydrogeomorphic disturbance and sediment
417 burial, with diverse propagation modes and the possibility of clonal growth after
418 breakage (Gastaldo, 1992; Pfefferkorn *et al.*, 2001; Allen and Gastaldo, 2006). Such
419 plants may have spread upstream along the energy gradient, and consequently may
420 have contributed to the modulation of fluvial landforms directly from inside river channels
421 along both longitudinal and transverse river dimensions.

422 By the end of the Carboniferous, the full range of the most abundant fluvial
423 biogeomorphic types seen on the Earth surface today had evolved (Davies and Gibling,
424 2013). The great expansion of riparian forests along longitudinal and transverse river
425 gradients, which occurred during the Carboniferous, led to a large increase in substrate
426 cohesion and landscape roughness, and thus to storage of fine sediment and organic
427 matter, at the scale of the entire fluvial corridor.

428 Vegetation thus drastically modified fluvial landform dynamics within lowland-plain
429 reaches with low to medium energy. By the Early Pennsylvanian, the widespread global
430 development of anastomosing rivers and the appearance of blackwater rivers (Fig. 5e
431 and 6) with single or multiple fixed channels filled with sand resulted in stable aggrading
432 muddy floodplains, which acted as important sinks for fluvial sediment, organic matter
433 and nutrients transported from the river channel to the adjacent floodplains (Davies and
434 Gibling, 2011). Davies and Gibling (2011, 2013) suggested that this threshold-crossing

435 change in fluvial geomorphology during the Mississippian was promoted by several
436 factors. These included the increasing arborescence and density of vegetation which
437 developed complex and diverse root systems, the possibility for vegetation to grow
438 directly in active channels and on above-water-table floodplain levees on dryland plains,
439 and the increased supply of large woody debris, promoting log jams and avulsive
440 behaviour within rivers.

441 In the late Carboniferous, vegetation colonized upland valleys and probably started to
442 spread within upland areas (Falcon-Lang and Bashforth, 2005; Gibling *et al.*, 2010).
443 Phillips and Lorz (2008) and Pawlik (2013) highlighted the ways in which vegetation can
444 affect upland rocks through weathering, pedogenesis, and the regulation of mineral and
445 organic matter transfer from hillslopes to river channels. At this time vegetation growing
446 along banks and within the active channel started to interact more intensively with
447 coarse bedload. The increase in the supply of large woody debris to river channels in
448 the piedmont zones would have favoured also the development of new biogeomorphic
449 types related to avulsion dynamics promoted by accreting pioneer vegetated points or
450 log jams. By promoting avulsions, pioneer vegetation growing directly in river channels
451 and accumulations of large woody debris contributed to the Pennsylvanian appearance
452 of wandering and island-braided types (Gibling *et al.*, 2010) (Fig. 5e and 6). As pointed
453 out by Tockner *et al.* (2003) and Gurnell *et al.* (2005), these biogeomorphic types are
454 characterised by a complex mosaic of habitat within a large active channel. In particular,
455 riparian islands initialised by pioneer vegetation or log jams often constitute >50% of the
456 active corridor. Pioneer islands contribute in creating points of matter aggregation, and
457 vegetation grows within a highly dynamic active tract (Gurnell *et al.*, 2001; Francis *et al.*,

458 2009). Church (2002) suggested that wandering and island-braided types are a
459 potentially persistent state marking the transition between braided and meandering
460 types, characterised by strong feedback dynamics between biota and abiotic elements
461 (Francis *et al.*, 2009).

462 Palaeontological evidence from the Pennsylvanian indicates that the biogeomorphic
463 partitioning of the riparian ecosystem was important at this time, with trees specialized
464 to different levels of hydrogeomorphic connectivity (Bashforth *et al.*, 2011). For example,
465 the lycopsid tree *Sigillaria* may have preferred partly disconnected habitats with periodic
466 substrate dryness whereas calamitalean trees, exhibiting a clonal behavior, were
467 adapted to moist and disturbed areas (Gastaldo, 1992). The spatial biogeomorphic
468 partitioning which occurred during the Pennsylvanian can be linked with biogeomorphic
469 succession dynamics (*sensu* Corenblit *et al.*, 2007). This period exhibits the earliest
470 palaeontological evidence for riparian succession associated with fluvial landform
471 construction. Smith (1962) noted vertical changes in spore content suggesting that plant
472 succession and vertical changes in substrate properties took place in parallel and
473 indicating temporal succession of riparian habitat conditions (Greb *et al.*, 2002). During
474 this interval, competition between riparian tree species may have become an important
475 selection pressure within aggraded and stabilized floodplain levees. Competition
476 between riparian tree species and tree species spreading from uplands into the
477 floodplain margins also may have imposed new selection pressures. These selection
478 pressures may have favoured the development of K-traits such as increased height with
479 developed canopies for accessing light, deep roots for accessing water, and as reported
480 by Chaloner and Sheerin (1951) an increase in the size and quality of seeds.

481 The widespread engineering of fluvial systems by new and diverse plant communities
482 also promoted the creation of new niches for a variety of newly evolved fauna. The
483 major Palaeozoic diversifications in fluvial style (namely at the Silurian-Devonian and
484 Mississippian-Pennsylvanian boundaries) closely correspond with major expansions in
485 terrestrial faunal biodiversity (Davies and Gibling, 2013).

486

487 *Post-Palaeozoic: toward a global spread on continents by seed plants*

488

489 Following the Carboniferous, a major innovation directly related to seed habit was the
490 ability of plants to spread on upland surfaces (Fig. 5e). Seed plants became dominant
491 during the Permian. By the Upper Permian, more than 60% of the Earth's known flora
492 was composed of gymnosperm species, which spread globally on continents and
493 exhibited palaeogeographic partitioning from low to high latitudes and from wet to dry
494 and warm to cold biomes. These Permian biomes fluctuated in space according to
495 global climatic changes, particularly as the assembly of the global supercontinent
496 Pangea resulted in a worldwide increase in aridity, slowly spreading from present-day
497 North America, through Europe, and into Asia as the Permian progressed (Greb *et al.*,
498 2006). Many Permian river systems are likely to have been significantly influenced by
499 this global aridity and its associated reduction of global vegetation cover (e.g. an
500 increase in braided river planforms).

501 After the Palaeozoic, other major innovations in vegetation arose, though the precise
502 effects of these on the eco-evolutionary history of rivers is less well studied. One major
503 Mesozoic innovation was the Cretaceous rise of angiosperms (flowering plants).

504 Angiosperms, comprising diverse kinds of trees, shrubs and herbs, have dominated the
505 majority of terrestrial habitats since at least the earliest Paleocene. The ancestors of
506 angiosperms were probably herbaceous weedy shrubs with a rapid life cycle (Crane,
507 1987; Friis *et al.*, 1999, 2001). Based on a molecular study, Qui *et al.* (1999) suggested
508 that the basal group of angiosperms is Nymphaeales, which are aquatic rhizomatous
509 herbs. The Cenozoic also saw a major evolutionary step in the history of vegetation,
510 with the rise and spread of grasses, which may also have first evolved in the latest
511 Mesozoic (Greb *et al.*, 2006). The effect of the rise of grasses on river morphology
512 during this period was not studied yet and certainly represents a future challenge.

513 During the Quaternary period huge climatic fluctuations also modulated the spatial
514 distribution of biogeomorphic types, leading to fluvial metamorphosis as documented
515 mainly in the northern hemisphere (e.g. Baker and Penteado-Orellana, 1977). For
516 example, it was shown that the spatial pattern of *Populus* spp. (e.g. *P. nigra* L.), which
517 are keystone ecosystem engineers within temperate rivers (Gurnell and Petts, 2006),
518 fluctuated during the Quaternary according to the successive ice ages (Bennett *et al.*,
519 1991). Cottrell *et al.* (2005) showed that populations of *P. nigra* remained during the last
520 ice age, between 100 000 and 10 000 BP, in southern Spain, southern Italy and the
521 Balkans. The species succeeded in recolonizing north and central European fluvial
522 corridors during the Holocene.

523 Even though the repartition of the different biogeomorphic types around the world
524 varied greatly according to geological, climatic and anthropogenic changes, the
525 potentially available biogeomorphic types, which emerged from the late Silurian to the
526 Carboniferous, remained the same.

527

528 **Today's eco-evolutionary effects on biogeomorphic structure and stability along**
529 **the river dimensions**

530

531 It is the ligneous angiosperms, originating in the Mesozoic and evolving toward extant
532 herbs, riparian shrubs and trees, which currently most drastically affect
533 hydrogeomorphic parameters and river morphology along the longitudinal, transverse
534 and vertical dimensions of the river corridor (Gurnell, 2014; Corenblit *et al.*, 2014). Many
535 phenological, physiological, morphological and biomechanical traits of contemporary
536 riparian angiosperms are specifically related to river patterns and processes (Lytle,
537 2001; Karrenberg *et al.*, 2002; Lytle and Poff, 2004; Bornette *et al.*, 2008; Puijalon *et al.*,
538 2011). The successive adaptations improved the resistance and resilience of
539 contemporary riparian plants within the naturally disturbed fluvial environment and thus
540 increased their capacity to modulate their geomorphic environment during floods
541 (Gurnell, 2014). Modern plant traits that improve tolerance to long-term submersion and
542 sediment burial include height, floatability, and production of adventitious roots, and
543 these traits are preferentially selected within downstream low-energy river sections with
544 cumulatively more discharge and turbidity (Naiman and Décamps, 1997; Karrenberg *et*
545 *al.*, 2002; Lytle and Poff, 2004). Additional plant traits improve mechanical resistance
546 (i.e. tolerance or avoidance) to breakage and uprooting, including a small to
547 intermediate size, flexible stems, breaking points (Beismann *et al.*, 2000), deep rooting,
548 and a high resilience after disturbances. Adaptations to fluvial disturbance reinforcing
549 vegetation resilience include for example the ability to reach sexual maturity over a short

550 period, production of numerous buoyant seeds, capability to resprout, and adequate
551 timing of seed production according to the natural flow regime (Mahoney and Rood,
552 1998). Such additional traits were selected within more energetic intermediate to
553 upstream bedload river sections.

554

555 *Plant traits modify fluvial types and related landform resistance and resilience*

556

557 In modern rivers, as a result of the ability of vegetation through physiological or
558 mechanical adaptations to resist hydraulic constraints and colonize bare alluvial
559 surfaces between large infrequent floods, fluvial landforms increased relative elevation,
560 the percentage of fine-sediment content and their resistance to erosion (Bertoldi *et al.*,
561 2011a; Gurnell, 2014). Taking into account the key role of vegetation in modern river
562 geomorphology, *fluvial biogeomorphic types* (FBT) may be considered as the second of
563 two overall *fluvial types*. The first type is mineral-dominated where riparian vegetation
564 does not significantly control the geomorphology, whilst the second is the *fluvial*
565 *biogeomorphic type* where riparian vegetation largely modulates or controls channel and
566 floodplain geomorphology.

567 These two types may be subdivided further into several categories. Two categories of
568 mineral-dominated fluvial types can be identified in upstream sections in which hydraulic
569 forces exceed the resistance capabilities of plants: straight-entrenched in torrential
570 production zones and braided in transfer zones (Table 2). Four categories of contrasted
571 fluvial biogeomorphic types exist within large rivers, each with characteristic modulations
572 of the balance between cohesive and destructive forces: island-braided, wandering,

573 meandering, and anastomosing (Table 2). Several functions such as sediment, nutrient
574 and organic-matter retention and transformation are modulated differently according to
575 the biogeomorphic type. Specific spatiotemporal modulations of hydrogeomorphic stress
576 and disturbance and biotic interactions and diversity are also related to each
577 biogeomorphic type (Gurnell, 2014).

578 Thresholds in fluvial landform remobilisation related to FBT do not solely depend on
579 intrinsic sediment cohesiveness and flood magnitude and frequency, as was the case
580 before the colonization of continents by plants. As pointed out by Gurnell (2014), fluvial
581 landform erosion or removal thresholds are strongly modulated by vegetation resistance
582 traits. Due to stabilization by roots, fluvial landforms are more resistant to erosion during
583 floods. They are also resilient between large infrequent destructive floods where the rate
584 of vegetation growth and related engineer effects exceeds the frequency of destructive
585 floods (Francis *et al.*, 2009; Corenblit *et al.*, 2010; Bertoldi *et al.*, 2011b). As suggested
586 by Corenblit *et al.* (2007, 2011) and Gurnell *et al.* (2012), along the longitudinal
587 dimension, the strength of abiotic-biotic feedbacks leading to an increase of
588 biogeomorphic resistance and resilience reaches its maximum within large rivers at
589 intermediate levels of hydrogeomorphic disturbance, mainly in meandering, wandering
590 and island-braided sections with low to high stream power (approximately 10 to 300
591 W m^{-2}) (Table 2). Biogeomorphic feedbacks in these sections can lead under certain
592 circumstances to abrupt changes in fluvial pattern often interpreted in fluvial
593 geomorphology as ‘fluvial metamorphoses’ (Schumm and Lichty 1963; Schumm, 1969;
594 Gurnell and Petts, 2002; Tal and Paola 2010). These changes are represented in the
595 landscape by (i) biogeomorphic types dominated by sediment deposition and vegetation

596 succession (e.g. meandering and anastomosing types); (ii) biogeomorphic types
597 dominated by erosion and vegetation rejuvenation (e.g. island-braided type); or (iii)
598 transient patchy metastable states (e.g. wandering type). The different types represent a
599 combination of variations in discharge and sediment load, and are related to the
600 thresholds of vegetation resistance to floods or stress (e.g. drought), to their resilience
601 abilities, and to their landform construction effects (i.e. their effect and response
602 functional traits).

603

604 *A scale-dependent feedback controls the repartition of constructive and destructive*
605 *forces*

606

607 The fluvial biogeomorphic succession was identified by Francis *et al.* (2009) as a scale-
608 dependent feedback that produces characteristic landscape patterns (i.e.
609 biogeomorphic types) related to the strength of abiotic-biotic feedback along the energy
610 gradient (Corenblit *et al.*, 2009b; Francis *et al.*, 2009) (Fig. 7a). Levin and Segel (1985)
611 and more recently Rietkerk and Van de Koppel (2008) pointed out that self-organized
612 spatial structures (here e.g. fluvial islands) and patterns (here e.g. island-braided or
613 meandering biogeomorphic types) originate from local interactions between physical
614 processes and biota in diverse environments. Francis *et al.* (2009) suggested that short-
615 range activation (i.e. within and downstream of pioneer vegetation patches) and long-
616 range inhibition (i.e. around vegetation patches) are the basic FBS principles within
617 flood disturbed corridors (Fig. 7b). However, such fundamental present-day interactions
618 would not have been as prevalent in ancient environments before or during the

619 evolution of land plants (Davies and Gibling, 2013). For such situations it is possible to
620 conceptually modify the FBS for different time intervals.

621 Once established, pioneer riparian plants with sufficient biomass interact with water
622 and sediment flow, and enhance a short-range positive feedback of accumulation of fine
623 sediment, organic matter, nutrients and diaspores within or immediately downstream
624 from vegetation individuals and patches (Gurnell *et al.*, 2005; Corenblit *et al.*, 2009b).
625 The cumulative local improvement of habitat conditions for vegetation and landform
626 stabilization within pioneer islands or on accreting point bars in turn favours organic
627 matter production, retention and nutrient consumption by plant communities. Vegetation
628 growth is accompanied in time by a succession of different categories of plant species,
629 shifting on the transverse and vertical dimensions from the dominance of r-strategists
630 (opportunists) to K-strategists (competitors *sensu* Grime, 2001) (Bornette *et al.*, 2008;
631 Tabacchi *et al.*, 2009) (Fig. 1). This self-reinforcing process of landform construction and
632 associated vegetation succession during the FBS is regulated through the progressive
633 disconnection of laterally and vertically accreting fluvial islands and floodplain levees
634 from hydrogeomorphic disturbances (Bendix and Hupp, 2000; Corenblit *et al.*, 2009b).
635 Short-range activation is accompanied by long-range inhibition of vegetation
636 development because water flow is diverted and concentrated around vegetated
637 patches or on opposite banks (Gurnell *et al.*, 2005; Francis *et al.*, 2009).

638 The spatiotemporal intensity and repartition of short-range activation and long-range
639 inhibition along the longitudinal energy gradient defines the biogeomorphic type, with a
640 characteristic patchy fluvial landscape in river sections with an intermediate level of
641 disturbance (Fig. 7 and 8). Highly energetic straight entrenched and braided types lack

642 short-range activation because vegetation does not persist within these highly disturbed
643 systems (Fig. 7 and 8; Table 2). These fluvial types are dominated by small short-lived r-
644 strategists that will only affect topography sporadically at a micro-scale. The island-
645 braided and wandering types exhibit a shifting mosaic of activation zones (i.e. islands of
646 fertility) corresponding to accreting pioneer islands and floodplain levees, with inhibition
647 zones around pioneer islands and at the margins of floodplain levees. The landscape
648 complexity within these types is strong and contributes to high habitat and species
649 diversity within the fluvial corridor (Ward and Stanford, 1983; Amoros and Bornette,
650 2002; Tockner *et al.*, 2003; Gurnell *et al.*, 2005, 2009). These biogeomorphic types
651 encompass a mixture of r- and K-strategists within a shifting mosaic with a high turnover
652 (Fig. 7 and 8; Table 2). The single free meandering type is characterized by a
653 concentration of the short-range activation zone on migrating point bars where pioneer
654 riparian vegetation becomes established, traps sediment and builds the floodplain (Fig.
655 7 and 8; Table 2). Long-range inhibition is located on the opposite bank which is
656 regularly eroded, leading to meander cutoff and the formation of oxbow lakes.
657 Anastomosing rivers are dominated by a slight activation on river margins where fine
658 sediment tends to be deposited during floods (Fig. 7 and 8; Table 2). Because the
659 stream power is low in such lowland river sections, long-range inhibition is weak. Such
660 stable biogeomorphic types with a low turnover (Table 2) are dominated by K-
661 strategists.

662

663 *The scale-dependent feedback enhances a niche partitioning of the riparian ecosystem*

664

665 Many palaeontological studies have shown that the modification of the fluvial
666 environment, driven by vegetation dynamics from the late Silurian to the Carboniferous
667 (Davies and Gibling, 2010, 2013), was accompanied by a diversification of plant and
668 faunal ecological strategies and assemblages within fluvial corridors (Beerbower, 1985;
669 Buatois *et al.*, 1998; Labandeira, 1998; Driese *et al.*, 2000; Benton, 2010; papers in
670 Vecoli *et al.*, 2010). This would have resulted in the potential for active construction of
671 new habitats, permitting the organization of contrasted biogeomorphic domains within
672 rivers. Feedbacks between vegetation traits and hydrogeomorphic processes lead, in
673 modern rivers, to the development along the longitudinal energy gradient of a patchy
674 fluvial landscape encompassing different kinds of biologically engineered landforms
675 such as stabilized or migrating narrowed channels, accreting vegetated point bars,
676 fluvial islands, benches, floodplain levees and oxbow lakes. Such varied habitats
677 support characteristic plant and faunal assemblages in different areas of the fluvial
678 corridor, different seasons or succession stages and support high levels of diversity
679 (Amoros *et al.*, 1987b; Pautou and Arens, 1994).

680 During the cycle of biogeomorphic succession, landform construction and related
681 modifications of the gradient of hydrogeomorphic connectivity and habitat conditions
682 provide new opportunities, for example for shade-tolerant riparian competitive plant
683 species to become established within the fluvial corridor after destructive floods
684 (Johnson *et al.*, 1976; Naiman *et al.*, 2005). The duration and spatial extent of these
685 opportunities generally increase downstream along the gradient of energy. We stress

686 that, because the physical and chemical environment is adequately modified by plants
687 during the FBS cycle, many aquatic and terrestrial plants and micro- to macro-faunal
688 elements coexist currently within fluvial corridors, or start to become established on a
689 temporary or more durable basis in intermediate to high energy reaches. For example,
690 channel avulsions provoked by vegetation and large woody debris increase the
691 formation of secondary, abandoned channels and oxbow lakes. Many aquatic and semi-
692 aquatic plants, fauna and micro-organisms find refuge during stressful periods within
693 these geomorphic units (Tabacchi *et al.* 2009; Stella *et al.*, 2011).

694 As observed by Stallins and Parker (2003) in the context of barrier-island dune
695 systems, plant-engineered geomorphic gradients are partitioned into a set of spatially
696 organized biogeomorphic domains with characteristic interactions between allogenic
697 (hydrogeomorphic) and autogenic (biological) processes. Based on observations in
698 different disturbed biogeomorphic systems under the control of engineer plants –
699 respectively vegetated sand dune and riparian systems – Stallins (2006) and Corenblit
700 *et al.* (2007) reached similar conclusions about how species strategies and plant
701 assemblages operate locally along geomorphologically constructed gradients. Previous
702 models had suggested passive adaptations to stress and physical disturbance as the
703 sole operational mechanism, but these authors proposed active construction of new
704 habitats disposed along the biologically modulated longitudinal, transverse and vertical
705 gradients. We stress that the current hydrogeomorphic gradients and related ecological
706 strategies (see Bornette *et al.*, 2008) (Fig. 9a) observed along temperate fluvial corridors
707 are modulated in the long term through a complex relationship between engineer
708 populations, community assemblage, landform-mediated disturbance gradient and

709 hydrogeomorphic disturbance regime. This assessment contrasts with a modulation
710 based on the one-way respective causal importance of these factors, as proposed in
711 earlier models of river continuum (Vannote *et al.*, 1980) and flood pulse (Junk *et al.*,
712 1989).

713 This effective niche partitioning of the riparian ecosystem by engineer plants takes
714 place through time as a fluvial biogeomorphic succession in which the *geomorphic*
715 *phase* is a rejuvenation phase. The *pioneer* and *biogeomorphic phases* are resilient
716 transient states toward *the ecological phase* which is a resistant attractor domain (Fig.
717 9b). At initial stages of the FBS, pioneer herbaceous and shrubby plants, establishing
718 on alluvial bars, enhance the deposition of mineral and organic matter and thus
719 landform construction in the highly connected biogeomorphic domains of the various
720 biogeomorphic types (Corenblit *et al.*, 2009a,b) (Fig. 1). Along the longitudinal energy
721 gradient ('disturbance frequency' in Fig. 9), vegetation trapping sediment and stabilizing
722 fluvial landforms thus actively contributes to modulate the repartition of resistant
723 strategies (according to anoxia and sediment burial) and resilient strategies (according
724 to mechanical constraints) (Fig. 1). Channel stabilization and the growth of islands and
725 floodplains in river sections where the strength of abiotic-biotic feedback is strong
726 enhance the formation of a well structured transverse gradient of hydrogeomorphic
727 connectivity, leading to distinctive biogeomorphic domains adjacent to each other and
728 separated by ecotones (*sensu* Naiman et Décamps, 1997) (Fig. 1). These
729 biogeomorphic domains are different from the four fluvial biogeomorphic types defined
730 above (see Table 2).

731 The definition of biogeomorphic domains, which are necessarily characterized by the
732 presence of vegetation, are based on submersion duration and frequency along the
733 transverse gradient (Bornette *et al.*, 2008; Tabacchi *et al.*, 2009) (Fig. 1), whereas the
734 biogeomorphic types are defined along the longitudinal gradient. Two main
735 biogeomorphic domains are identified: (i) an unstable disturbed riparian environment
736 highly exposed to hydrogeomorphic disturbances and where the ecosystem is highly
737 resilient (dominated by r-strategists); and (ii) a stabilized and partly disconnected
738 riparian environment engineered by vegetation with increased resources, pedogenesis
739 and where the ecosystem is more resistant (dominated by K-strategists). Corenblit *et al.*
740 (2009a,b) succeeded in relating such transverse niche partitioning to sediment trapping
741 by engineer plants on the River Tech. The authors showed a significant variation in plant
742 community structure between the two process domains with (i) a very strong diversity in
743 the highly disturbed domain dominated by r-strategists; and (ii) a decreased diversity in
744 the constructed domain dominated by K-strategists. However, Ward and Tockner (2001)
745 noted that, as an ecological consequence, the spatiotemporal juxtaposition of habitats
746 with contrasted conditions and strategies greatly contributes to increase gamma
747 diversity within fluvial corridors. This increase is evident both along the longitudinal
748 energy gradient and along the transverse gradient of connectivity at intermediate levels
749 of disturbance as suggested in Connell's (1978) intermediate disturbance hypothesis.

750 The unstable disturbed domain is subjected in high-energy reaches to frequent
751 sediment scouring and bedload transport while fine sediment and organic matter tend to
752 be deposited within pioneer vegetation patches leading to the emergence of the
753 stabilized and partly disconnected domain. Consequently, biochemical and

754 biogeochemical processes also vary drastically within these two domains (Naiman and
755 Décamps, 1997). Anaerobic processes such as denitrification are generally effective
756 within the vegetated domain during the biogeomorphic and ecological phases (Pinay *et*
757 *al.*, 2000). Nitrate removal from interstitial waters is efficient and rapid within the plant-
758 engineered environment (for a review see Fisher *et al.*, 2007). The engineered domain
759 thus may be considered at the scale of the fluvial corridor as nitrogen sinks. In
760 accordance with the view of Fisher *et al.* (2007), we suggest that developing a general
761 understanding of flowpath biochemistry that encompasses the diversity of
762 biogeomorphic domains in which dissolved matter are transported by water and uptake,
763 stored and transformed by organisms (bacteria, fungi, plants and animals) may become
764 a priority.

765 This position suggests that biogeomorphic alternative types largely differ in their
766 functional attribute. In particular, sediment and nutrient retention in pioneer vegetated
767 patches may promote above - and below - ground production in association with a larger
768 nutrient pool (Fisher *et al.*, 2007) and consequently feed back on the geomorphic
769 structure by further enhancing fine sediment retention (i.e. short range activation) and
770 topographic changes (Bendix and Hupp, 2000).

771

772 **Eco-evolutionary model**

773

774 This review suggests that the path-dependent history of reciprocal interactions and
775 adjustments between the evolution of riparian vegetation and fluvial geomorphology
776 needs to be brought into an eco-evolutionary perspective (*sensu* Erwin, 2008; Post and

777 Palkovacs, 2009; Matthews *et al.*, 2014) As pointed out by Gibling and Davies (2012), a
778 hierarchy of evolutionary and self-organisation feedbacks between riparian vegetation
779 and fluvial geomorphology occurred along the three spatial gradients, mainly from the
780 mid Silurian to the late Carboniferous (c. 430-299 Ma) which represents the period in
781 Earth history when the development of complex non-marine ecosystems began to reach
782 its culmination (see also Davies and Gibling, 2013).

783 Wright (2009) and Wright *et al.* (2012) stressed that engineer species almost certainly
784 change selection pressures in largely modified environments through niche construction
785 (NC) (*sensu* Laland *et al.*, 1999; Odling-Smee *et al.*, 2003). NC refers to the case when
786 the evolutionary dynamics of the engineer species or others species within the
787 ecosystem are modified through changes in one or more dimensions of the physical
788 environment (Matthews *et al.*, 2014). By definition, NC operates with an evolutionary
789 response within the ecosystem engineered by living organisms. Alluvial landforms
790 durably engineered by organisms were considered by Steiger and Corenblit (2012) as
791 the signature of feedback between hydrogeomorphic processes and plant evolution,
792 supporting the emergence of what they have called 'evolutionary geomorphology'.

793 As highlighted above, the long-term effects of riparian niche-constructing plant
794 species on fluvial environments are, at the scale of the fluvial corridor, large and
795 durable. Throughout Earth history, the first appearance of engineer plants, and thus the
796 persistence or systematic recurrence of specific kinds of modified (biologically
797 constructed) riparian habitats, would have been a major selective force for plant
798 functional traits and ecological strategies within partitioned riparian ecosystems (Fisher
799 *et al.*, 2007; Gibling and Davies, 2012; Davies and Gibling, 2013). Hydrogeomorphic

800 parameters (e.g. topography, sediment texture, hydrogeomorphic connectivity) adjusted
801 as the engineer-traits of plants evolved, particularly from the end of the Silurian
802 onwards. In turn, this adjustment continually influenced plant evolution and riparian
803 ecosystem structure and function, ultimately leading to the emergence of riparian
804 ecosystems (Fig. 10).

805 By considering the degree to which the FBS model could be applied at different
806 intervals of the evolutionary history of terrestrialization linked to land plants, Davies and
807 Gibling (2013) suggested that, prior to the colonization of continents by land plants in
808 the Ordovician, river systems were permanently in the *geomorphic phase* of the FBS
809 because no pioneer vegetation could colonize a river after flood (Fig. 10). As such,
810 fluvial landforms only adjusted according to geological, geomorphic and hydrological
811 controls. According to Davies and Gibling (2013), the *pioneer phase* of the FBS
812 theoretically could be attainable only after the appearance of the first riparian
813 embryophytes (Fig. 10). This phase became possible due to the first abundant
814 generations of small, primitive, rooted pioneer land plants, capable of responding to
815 immersed conditions and to an unstable and fluctuating fluvial environment. The
816 *biogeomorphic phase* of the FBS was probably not achieved until after the late Silurian
817 to earliest Devonian (Fig. 10). This phase was characterized by strong eco-evolutionary
818 feedbacks between vegetation evolution and hydrogeomorphology with the appearance
819 of new biogeomorphic types and a second generation of biotic responses (e.g. the
820 evolution of deeper roots) related to a constructing and stabilizing riparian environment.
821 Davies and Gibling (2013) suggested that the *ecological phase* of the FBS could only be
822 reached from the Carboniferous onwards, once a third generation of selective plant

823 traits, related to colonizing an aggraded and stabilized riparian environment, had
824 evolved (Fig. 10).

825 These successive generations of biotic selections and related geomorphic changes
826 finally resulted in the emergence of the main fluvial biogeomorphic types (FBT)
827 observed today (Table 2). Contemporary fluvial hydrosystem gradients and associated
828 community structure and function emerged from these long-term feedback dynamics
829 between vegetation evolution and river dynamics (Fisher *et al.*, 2007; Corenblit *et al.*,
830 2009b). The related gradients of ecological strategies observed along spatial and
831 temporal river dimensions probably arose from evolutionary trade-offs and cost-benefit
832 among plant species in an environment in which stabilized and disconnected domains
833 developed progressively at the margins of disturbed and unstable domains. The
834 concepts of NC and ecological inheritance (*sensu* Odling-Smee *et al.*, 2003) appear to
835 be potentially useful in describing such dynamics (Gibling and Davies, 2012; Corenblit *et*
836 *al.*, 2014). Francis *et al.* (2009) and Corenblit *et al.* (2009b, 2014) suggested that certain
837 fluvial landforms engineered by pioneer riparian species, such as fluvial islands and
838 benches, improve the fitness of the engineer species themselves, as well as other
839 species within the ecosystem. Rood *et al.* (2011) recently demonstrated that fine-
840 sediment deposition favours willow establishment and clonal expansion, and that the
841 canopies protect and trap sand in a feedback that sustains surface sand and sand-bar
842 willows. Such landforms are beginning to be considered as positive niche constructions,
843 and thus as functional ecological components of the fluvial hydrosystem (Fisher *et al.*,
844 2007; Corenblit *et al.*, 2010, 2011, 2014).

845 Niche-constructed habitats and gradients also lead to very important and recurrent
846 modifications at ecological timescale in species interactions and community traits within
847 the riparian system (Corenblit *et al.*, 2009a,b). The way in which modern aquatic and
848 riparian plant, animal and micro-organism communities organize along the longitudinal
849 gradients of energy and transverse connectivity gradients reflects millions of years of
850 engineering by vegetation (Bashforth *et al.*, 2011). We stress that, at the scale of the
851 landscape, aquatic and riparian community assemblages, diversity, resistance and
852 resilience along engineered hydrogeomorphic gradients may be considered emergent
853 properties of a complex biogeomorphic adaptive system (*sensu* Holling, 1973; Levin,
854 1998). These properties have an evolutionary history that stretches back at least 420
855 million years.

856

857 **Concluding remarks**

858

859 This review paper suggests that a fuller comprehension of riparian ecosystem structure
860 and stability depends on our ability to conceptualize and analyze both ecological
861 (contemporary) and evolutionary (ancient) feedbacks. Such feedbacks operate between
862 small-scale biological phenomena (genotypic selection and phenotypic expression of
863 biological traits at the organism/population level) and patch-scale hydrogeomorphic
864 processes (fluvial landform adjustment).

865 A huge conceptual, methodological and technical research effort still remains to be
866 carried out at the interface between several disciplines to integrate the evolutionary
867 dimension of rivers within a four-dimensional framework. One difficulty will be to identify

868 the ecosystem integration levels affected by engineer activities. Dawkins (2004) and
869 Matthews *et al.* (2011) indeed pointed out that evolutionary responses of populations to
870 engineer activities within an ecosystem may be varied. The engineer species itself may
871 be concerned exclusively, with the selection of new anatomical, physiological or life-
872 history traits related to its niche construction, or even the selection of engineer-alleles
873 that improve the ability to construct niches (extended phenotype *sensu* Dawkins, 2004).
874 Evolutionary responses may in other cases concern only other species present in the
875 ecosystem; they may even provide a feedback to the engineer species through the
876 selection of alternative traits for other species that influence the engineer species, for
877 example through predation, competition, or symbiosis. These examples are only some
878 among many theoretical possibilities of combinations of eco-evolutionary interactions
879 within the riparian system.

880 We suggest that forging a classification or hierarchy of eco-evolutionary interactions
881 within the riparian context represents a fundamental step toward the integration of
882 abiotic-biotic feedbacks within the four-dimensional framework of river dynamics.
883 Concepts set out in the niche construction framework will also have to be formulated as
884 operational working hypotheses to be tested in ways suggested by Corenblit *et al.*
885 (2014).

886

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888

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1357

1358 **Tables**

1359

1360 Table 1. Correlation matrix between the different parameters and between axis 1 and

1361 axis 2 of the canonical correspondence analysis (CCA) (biplot in Figure 3).

	Species (axis 1)	Species (axis 2)	Hydrogeo. (axis 1)	Hydrogeo. (axis 2)
Species (axis 1)	1.00	-0.01	0.99	0.00
Species (axis 2)	-0.01	1.00	0.00	0.96
Altitude	-0.84	0.17	-0.85	0.17
Submersion duration	0.87	-0.34	0.88	-0.36
D ₁₆	0.02	0.65	0.02	0.68
D ₅₀	0.06	0.73	0.06	0.75
D ₉₀	0.55	0.56	0.55	0.58

1362

1363

1364 Table 2. Description of the main fluvial and biogeomorphic types. F/D ratio: F = rate of landform formation; D = rate of landform

1365 destruction (see Corenblit *et al.*, 2011, Jones *et al.*, 2012).

Biogeomorphic type / *fluvial type	Description	Specific stream power range ($W m^{-2}$)	Width/dept h ratio	Sediment dynamics	Vegetation control on fluvial morphology	Landform/ succession turnover	F/D ratio	Dominant plant adaptation	Dominant plant strategy within the fluvial corridor
*Straight-entrenched	Straight step channel directly connected to hillslopes.	>300	Very low <10	Bedload	Bank stabilization	<1 year	>1	Size	r
*Braided	Multiple unstable channels separated by instable bars; shaped mainly by physical processes.	>300	High >40	Bedload	Negligible	<1 year	<1	Size	r
Island-braided	Braided rivers with vegetated islands storing fine sediments, nutrients and organic matter; very high habitat turnover enhancing high landscape heterogeneity.	100 – 300	High >40	Bedload / mixed load	Intermediate	Few to 15-20 years	<1	Size/biomechanical	r
Wandering	Transition between island-braided and meandering styles; characterized by growing vegetated islands frequently	30 – 100	Intermediate 30 – 40	Bedload / mixed load	Intermediate	Few to 30-40 years	≈1	Size/biomechanical	r/K

connecting and disconnecting from the floodplain according to an active channel avulsion dynamics; high habitat turnover maintaining high landscape heterogeneity.

Sinuuous/meandering	Single channel rivers more or less sinuous; regular channel lateral migration; control of point-bar accretion and channel migration by vegetation; meander loops generally form neck- or chute cut-offs at the origin of oxbows.	10 – 30	Low 10 – 40	Suspended load	Strong	40-80 years	≈1	Size/biomechanical/physiological	K
Anastomosing	Rivers with stable multiple fixed channels separated by aggrading and densely vegetated islands; frequent avulsions lead to the creation of secondary channels and oxbows; vegetation contributes to stabilizing river banks and trapping fine sediment during large floods.	<10	Very low <10	Suspended load	Predominant	>80 years	>1	Physiological	K

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1367

1368 **Figure captions**

1369

1370 Figure 1. Model of fluvial biogeomorphic succession (FBS *sensu* Corenblit et al.,
1371 2007). The FBS encompasses four main phases of biological and geomorphic
1372 organisation (i.e. geomorphic, pioneer, biogeomorphic and ecological). The different
1373 phases .are located in this figure along the gradients of abiotic-biotic feedback
1374 strength, hydrogeomorphic connectivity, dominant strategy and biodiversity. The
1375 strength and the modality of interaction between vegetation and geomorphology are
1376 schematized in the figure, where V = vegetation; and G = geomorphology.

1377

1378 Figure 2. Illustration of the biogeomorphic succession pattern observed on the River
1379 Tech (Pyrenees, France). The biogeomorphic phase was characterized by a strong
1380 positive feedback of sediment stabilization, trapping and vegetation succession.
1381 Mean net topographic variation (recorded from 2002 to 2004 and resulting from 4
1382 flood events) within vegetation types A to H are illustrated with box and whisker
1383 plots; horizontal = median; lower and upper box limits = 25th and 75th percentile;
1384 whiskers extend to the 1st and 99th percentile; circles = outliers; stars = extreme
1385 points. During the FBS, dense herbaceous mats systematically contributed to
1386 sediment stabilization while ligneous communities trapped huge quantities of sand
1387 and diaspores (b). Mean topographic changes varied significantly between the
1388 different vegetation units (one-way ANOVA with repeated measures: $p < 0.0001$). V =
1389 vegetation and G = geomorphology. Such processes of landform construction
1390 enhanced hydrogeomorphic disconnection and vegetation succession. The pattern of
1391 vegetation succession was defined using a Hierarchical Cluster Analysis with the
1392 Bray-Curtis similarity index (a and c). Succession trajectories shown in (a) were

1393 defined according to changes in the similarity matrix in the interval between 2002
1394 and 2004. Modified from Corenblit *et al.* (2009b).

1395

1396 Figure 3. Canonical correspondence analysis undertaken on the River Tech floristic
1397 composition (plant species relative cover). 54% of the floristic structure was
1398 explained by the hydrogeomorphic variables modulated by engineer plants. Values
1399 indicate a very good correlation between axis 1 related to the hydrogeomorphic
1400 parameters and axis 1 related to the floristic composition ($r = 0.99$, Table 2). The
1401 correlation between both axes is also very good ($r = 0.96$, Table 2). The first
1402 canonical axis expresses a gradient of altitude, flood duration and D_{90} grain size. The
1403 correlation is negative with altitude height ($r = -0.84$, Table 2); positive with flood
1404 duration of ($r = 0.87$, Table 2); and positive with D_{90} ($r = 0.55$, Table 2). The second
1405 canonical axis expresses a gradient of sediment grain size (D_{16} , D_{50} and D_{90} , Table
1406 2). The correlation is positive with the three variables (D_{50} : $r = 0.73$, D_{16} : $r = 0.65$,
1407 D_{90} : $r = 0.56$, Table 2). CCA was performed with CANOCO v. 4.5.

1408

1409 Figure 4. The four-dimensional framework. In this framework, matter and energy
1410 fluxes are considered along four river-dimensions: (1) longitudinal; (2) transverse; (3)
1411 vertical; and (4) temporal.

1412

1413 Figure 5. Schematic representation of vegetation propagation within the fluvial
1414 system from the early Silurian to present. The emergence of new biogeomorphic
1415 types is underlined.

1416

1417 Figure 6. Evolution of the relative percentage of fluvial types from the Cambrian to
1418 the Carboniferous. Major aspects of plant evolution are indicated in the figure.

1419

1420 Figure 7. Conceptual model of scale-dependant feedback leading to the emergence
1421 of biogeomorphic types related to short-range activation and long-range inhibition:

1422 (a) relative % of the different biogeomorphic phases along the longitudinal (gradient

1423 of energy) and transverse (gradient of hydrogeomorphic connectivity) dimensions;

1424 (b) relative % of short-range activation and long-range inhibition along the

1425 longitudinal (gradient of energy) and transverse (gradient of hydrogeomorphic

1426 connectivity) dimensions; (c) changes in strength of abiotic-biotic feedback and

1427 related plant strategy along the longitudinal gradient. V = vegetation; and G =

1428 geomorphology.

1429

1430 Figure 8. Transverse repartition of the two biogeomorphic process domains with (i)

1431 high hydrogeomorphic connectivity dominated by r-strategists (resilient ecosystem);

1432 (ii) low connectivity dominated by K-strategists (resistant ecosystem). The different

1433 fluvial/biogeomorphic types are illustrated with satellite photographs taken from

1434 Google Earth™; SE: Salat River (France), 42°49'11"N, 1°11'30"E, 860m a.s.l.; B:

1435 Rakaia River (New Zealand), 43°52'26"S, 172°11'46"E, 15m a.s.l.; IB: Buëch River

1436 (France), 44°15'18"N, 5°51'11"E, 550m a.s.l.; W: Orco River (Italy), 45°12'12"N,

1437 7°50'50"E, 190m a.s.l.; M: Juruá River (Brazil), 6°29'03"S, 68°31'47"O; A: Ganges

1438 delta (India), 22°01'46"N, 89°00'50"E, 5m a.s.l..

1439

1440 Figure 9. (a) Static model of ecological processes controlling plant communities and

1441 related strategies. Modified from Bornette *et al.* (2008); (b) formulation of the

1442 previous model into a dynamic model of biogeomorphic processes controlling plant
1443 communities and related strategies. In this version vegetation is considered as an
1444 active adaptive component contributing to the construction of transverse/vertical
1445 gradients along the longitudinal dimension.

1446

1447 Figure 10. Biogeomorphic eco-evolutionary model of reciprocal interactions and
1448 adjustments between vegetation evolution and fluvial dynamics on geological time-
1449 scales. V = vegetation; and G = geomorphology.

1450