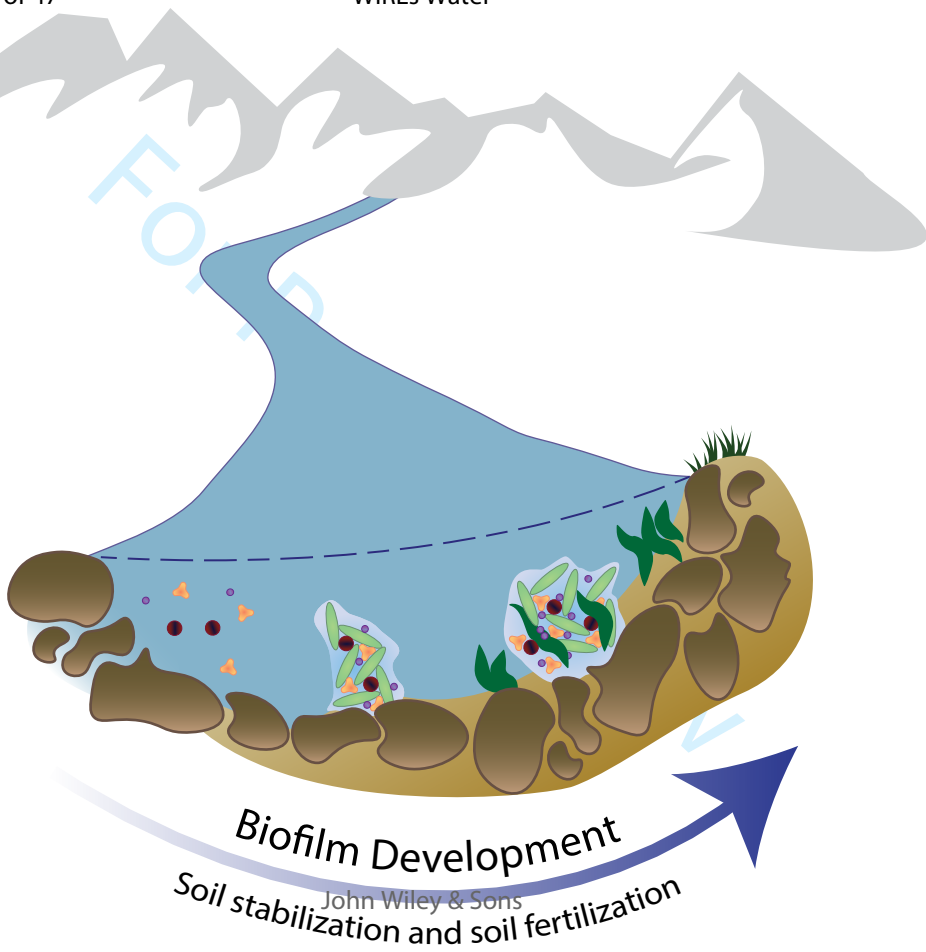Final accepted version of

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Biofilm Development

Soil stabilization and soil fertilization

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Article Title: **Ecosystem engineers: biofilms and the ontogeny of glacier floodplain ecosystems**

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Abstract

The term 'ecosystem engineering' emerged in the 1990s and is commonly used to refer to the activities of larger organisms like beavers and trees in rivers and streams. The focus on larger organisms may be motivated by their more visible effects on the environment. However, whilst it may be intuitive to suggest that the bigger the organism the bigger its potential engineering effects, there may be micro-scale organisms who through their number rather than their size can act simultaneously to result in significant impacts. This paper considers biofilms as a candidate ecosystem engineer. It is well known that biofilms play an important role in enriching the sediment matrix of nutrients and in stabilizing sediments. Biofilms may be critical in increasing the habitability of the benthic substratum. In this paper, we consider their potential role in the ontogeny of ecosystems in recently deglaciated terrain. We show how by changing sediment stoichiometry, decreasing sediment erodibility and reducing surface sediment permeability they may promote primary succession on lateral, incised terraces, which are less perturbed compared with the main active floodplain.

Graphical/Visual Abstract and Caption
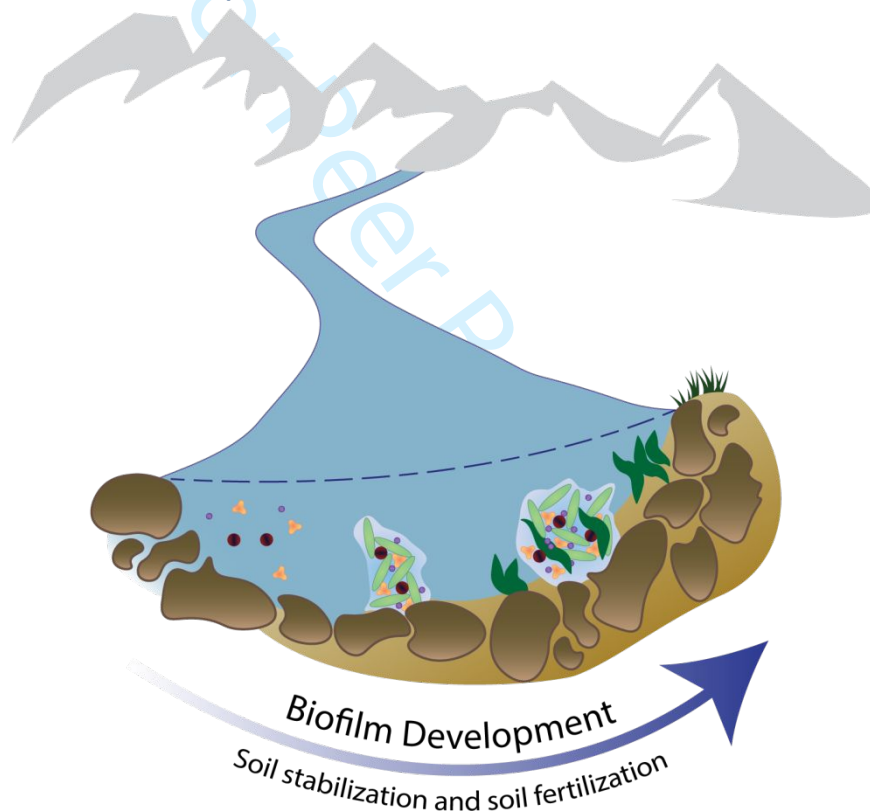
In streams, biofilms should be depicted as ecosystem engineers as they stabilize and fertilize sediments. Their development is thus critical for river ecosystems, particularly in glacier floodplains, where sediments tend to be unstable and nutrient-limited.

1. Introduction

Some organisms have the capacity to transform ecosystems echoing ways engineers build, create and modify their surrounding environment (Polvi and Sarneel, 2018). The term "ecosystem engineering", commonly used in ecology, describes this phenomenon and takes place in diverse ecosystems involving potentially a multitude of organisms (Jones *et al.*, 1994; 1997). In an introduction to ecosystem engineers in rivers, Polvi and Sarneel (2018) state that while the balance between hydraulic energy and sediment size and quantity influence the shape and function of streams, ecosystem engineers may considerably modify the functioning of aquatic and riparian ecosystems by changing streamflow characteristics. Freshwater ecosystem engineers can be found from headwaters downstream to estuaries, and in channels with different perimeter sedimentology (e.g., gravel, sand, and cohesive or coarse material), patterns (e.g., single-thread, braided) and morphodynamics. A stream's hydrological context may set constraints upon the growth and survival of ecosystem engineers in aquatic and riparian ecosystems (Gurnell, 2014; Bätz *et al.*, 2015) and organisms will generally only engineer positive feedbacks where resources are available (e.g., trapping and stabilizing fine sediments) within those constraints (Moore, 2006).

The floodplains of glacier-fed rivers, characterized by a recent switch to phototrophic conditions and extensive deposits of glaciogenic sediment, are usually slow to revegetate (Hotaling *et al.*, 2017a). Altitude, and hence temperature, may be a factor restricting vegetation succession, but fundamentally, glaciogenic sediments are nutrient-poor and unstable. Although conceptual models of vegetation succession in glacial forefields are well-developed (see review in Miller and Lane, 2019) the early stages of ontogenesis, and notably the role played by microbial life in driving related processes, is very poorly understood. Freshwater biofilms can develop rapidly and are implicated in multiple ecosystem processes (Battin *et al.*, 2003; 2016) and, because of the profound impacts that they can have upon resource availability, they are candidate ecosystem engineers. In this review, we focus upon freshwater stream benthic biofilms, as potential ecosystem engineers (Gerbersdorf *et al.*, 2008a; 2008b; 2009) with a particular focus on the early ontogeny of glacial floodplain ecosystems following glacier retreat. Biofilms have received less focus compared to more visible organisms such as beavers, mussels, and snails (Gurnell, 2014), and thus their engineering capacity is less well documented (Polvi and Sarneel, 2018). The aim of this paper is to review the role of biofilms as ecosystem engineers in streams and to develop a conceptual model for the relevance of microbial biofilms for glacial floodplain ecosystem ontogeny.

2. Ecosystem engineering: key concepts

2.1 The concept of ecosystem engineering

Almost three decades ago, two new terms emerged in ecology: 'ecosystem engineering' and 'ecosystem engineers' (Lawton and Jones, 1993; Jones *et al.*, 1994). The former describes the act of engineering an ecosystem, while the latter describes how organisms act as engineers (Jones *et al.*, 1994). The notion of ecosystem engineering and engineers in rivers and streams has been reviewed by Moore (2006) and more recently by Polvi and Sarneel (2018) and so only a short summary is provided here.

Jones *et al.* (1994) described ecosystem engineers as "*organisms that directly or indirectly modulate the availability of resources* […] *to other species, by causing physical state changes in biotic and abiotic materials*" (Jones *et al.*, 1994, p. 374). Jones *et al.* (1994; 1997) also introduced a key distinction between ecosystem engineers: autogenic *versus* allogenic. Autogenic engineers modify the surrounding environment through their own living or dead tissue (Jones *et al.*, 1994; Polvi and Sarneel, 2018). Allogenic engineers change the environment through the transformation of materials from one state to another (Jones *et al.*, 1994; 1997). As an example, vegetation (e.g., willows) plays an important role in the riparian zone (Gurnell and Petts, 2002) by stabilizing sediments and leading to the creation of more stable habitats like islands (Gurnell, 2014), as well as increasing bank stability (Simon and Collison, 2002). Hence, riparian plants are autogenic engineers as it is their own root system that increases the resistance of river banks to erosion. In contrast, caddisfly larvae build nets that reduce sediment erodibility by increasing the critical shear stress and hence resistance to sediment entrainment (Statzner *et al.*, 1999; Cardinale *et al.*, 2004; Johnson *et al.*, 2009). They are allogenic engineers as it is material made by the larvae that increases the resistance of gravels to erosion by water. The distinction between autogenic and allogenic engineers is not fixed; allogenic engineers can also have autogenic effects, and *vice versa* (Jones *et al.*, 1994), sometimes simultaneously. For instance, *Salix* autogenically increases the stability of river banks but allogenically changes depositional processes and can influence soil formation (Bätz *et al.*, 2015).

Ecosystem engineering is not concerned with direct provision of resources (e.g., as part of a food chain) (Jones *et al.*, 1994; 1997). For instance, predator-prey relationships between fish, such as salmonids, and macroinvertebrates, such as stoneflies, (Soluk and Richardson, 1997) are not engineering because prey simply provide food to predators. Rather, ecosystem engineers effectively manage resources; either intentionally or unintentionally. The former describes the traits ('extended phenotypes'; see Dawkins, 1982) that an organism possesses that allows intentional transformation of its environment (e.g., when a beaver explicitly builds a dam or the female salmon digs a redd) (Jones *et al.*, 1994; 1997). The latter describes the traces that have been left incidentally by organisms but which "manage" the environment for others (e.g., woody debris in the stream) (Jones *et al.*, 1994; 1997). Whether or not ecosystem engineering is intentional or unintentional, it is thought to occur in all ecosystems (Jones *et al.*, 1994) and the majority of, if not all, organisms are capable of doing it (Jones *et al.*, 1994; 1997; Wright and Jones, 2004).

Jones *et al.*'s statements about the ubiquity of ecosystem engineering opened a scientific debate about the usefulness of the terms 'ecosystem engineering' and 'ecosystem engineer';

4

108 what use is such terms if they apply everywhere and to all things (Reichman and Seabloom,
109 2002a; 2002b)? Ecosystem engineering needs to be distinguished in terms of scale and
110 magnitude of impacts and not simply based upon a functional definition regarding how an
111 organism engineers. Hence, we consider both functions and scale/magnitude effects.
112 Hastings *et al*. (2007) noted that ecosystem engineering impacts can be either small or
113 large, both in size and in time, and are related to the size and lifespan of the engineer itself.
114 Impacts should be important and visible at large scales for organisms to be true engineers of
115 ecosystems (Hastings *et al*., 2007). Intentional engineering may seem to be more important
116 than unintentional, but this is not necessarily the case. For instance, large woody debris,
117 which is unintentional engineering, can substantially impact salmonid populations (House
118 and Boehne, 1986; Zika and Peter, 2002).

119 **2.2 Stream ecosystem engineering: a matter of scale**

120 The physical processes that drive rivers and the ways in which rivers in turn erode and
121 deposit sediment to make landscapes have been identified at scales from the sub-daily to
122 millions of years (Schumm and Lichty, 1965). Such processes not only produce spatio-
123 temporal variation in the landscapes we see but also create the habitat templates upon
124 which life develops and also the constraints to which life must adapt (e.g., flow regime,
125 accommodation space, perturbation frequency, microclimate, etc.). At the same time, and
126 still poorly understood, organisms can modify stream ecosystems (Moore, 2006; Polvi and
127 Sarneel, 2018) through ecosystem engineering. Not all organisms have similar engineering
128 impacts on streams, and these effects depend upon the engineers themselves (Hastings *et
129 al*., 2007). Ecosystem engineering has tended to focus on visible impacts (e.g., beaver
130 dams) made by large organisms (see Gerbersdorf *et al*., 2009) but scaling stream
131 ecosystem engineers based on their size is not forcibly correct for three reasons.

132

133 First, within-organism size variations may be important and bigger individuals may have
134 bigger engineering effects. For instance, in relation to brown trout (*Salmo trutta*) redds,
135 bigger females produce bigger redds (Crisp and Carling, 1989). Redd construction, by
136 sorting sediments, decreases streambed erodibility by increasing the critical shear stress for
137 sediment transport (Montgomery *et al*., 1996). Thus, bigger female trout have bigger
138 engineering effects on the streambed compared with smaller females.

139

140 Second, scale depends upon your point of view. Depending on the chosen
141 geomorphological scale (e.g., watershed versus pool-riffle sequence) ecosystem
142 engineering can have substantial differences in apparent impacts. For instance, vegetation
143 might have a greater stabilization potential compared to caddisflies at the overall watershed
144 level, whereas for a given streambed surface caddisflies might have greater potential.
145 Hence, the smaller the scale, the more important smaller organisms become.

146

147 Third, there is an important relationship between engineering magnitude and the number of
148 organisms taking part in the engineering effort, and this association is generally positive and
149 may be more than additive. This is because it is the assemblage of organisms that multiply
150 the engineering potential of any individual organism (Boogert *et al*., 2006). Consider for
151 example microorganisms (e.g., microbes); individually they are not able to stabilize

5

152 sediments; in communities (biofilms) they may have remarkable stabilization effects (Section
153 3.2).

3. Stream biofilms as ecosystem engineers

3.1 Biofilms: an introduction

Biofilms dominate microbial life in most aquatic ecosystems (Flemming and Würtz, 2019) and particularly in streams (Battin *et al.*, 2016). Biofilms are surface-attached microbial communities that dwell in a matrix composed of extracellular polymeric substances (EPS). Several properties emerge from the biofilm mode of life that underpin its ecological success (Flemming *et al.*, 2016). The spatial organisation of microbial life within a matrix induces the establishment of physical and chemical gradients that provide habitat diversity and hence increases biodiversity. The biofilm matrix also facilitates the sorption of solutes and resource capture, stimulating biotic interactions and protecting from erosion, grazing and UV radiation, for instance.

Benthic biofilms in streams are highly diverse, including taxa from all three domains of life (that is, archaea, bacteria and eukaryotes) (Battin *et al.*, 2016; Bengtsson *et al.*, 2018) and even abundant and diverse viruses (Meriem Bekliz, personal communication). Prokaryotes and algae (mostly diatoms) rapidly colonize sedimentary surfaces where, after an initial adhesion phase, growth triggers a succession that often involves bacteria that are typical biofilm formers (Niederdorfer *et al.*, 2016). As this succession proceeds, niches can develop within the nascent biofilm, which fosters its biodiversity (Jackson *et al.*, 2001) (Figure 1).

Depending on local hydraulics and sediment size distribution, benthic biofilms form complex and dynamic physical structures, including ridges or filamentous streamers (in the centimeter range) that float in water (Flemming and Wingender, 2010). The physical structure of biofilms is critical for mass transfer and related microbial processes including the uptake and metabolism of organic compounds (e.g., Battin et al. 2003; Singer et al. 2010). It is the combination of the very large reactive surface, high biodiversity and continuous exposure to the flow of streamwater and associated solutes that make biofilms so important for stream ecosystem processes. For instance, they are the major sites of ecosystem metabolism (that is, gross primary production and respiration) and therefore of nutrient and carbon cycling in streams (Battin et al., 2016; Demars, 2018). As such, they also form the basis of the food web in numerous streams.

A critical aspect of biofilms is the matrix, extracellular material in which biofilms cells are embedded, acting as a protection for organisms (Flemming *et al.*, 2016). The matrix is also recognized to store all available material from lysed cells and to capture from the water phase both dissolved and particulate nutrients to make them available as nutrient and energy source (Flemming and Wingender, 2010). EPSs are the principal constituent of this matrix and is responsible for the biofilm's internal structure, surface attachment, and cohesion by maintaining cells in close proximity leading to strong cell-to-cell interactions (Flemming and Wingender, 2010). EPSs differ between biofilms in terms of nutrient availability, community composition, hydrologic forces and temperature. In their review, Flemming and Wingender (2010) describe the functions of EPSs bacterial biofilms. These include functions such as adhesion, aggregation, cohesion of biofilms, sorption of inorganic ions, enzymatic activity, nutrient source and water retention. It is thus possible to understand how the matrix can affect the mode of life of a given biofilm.
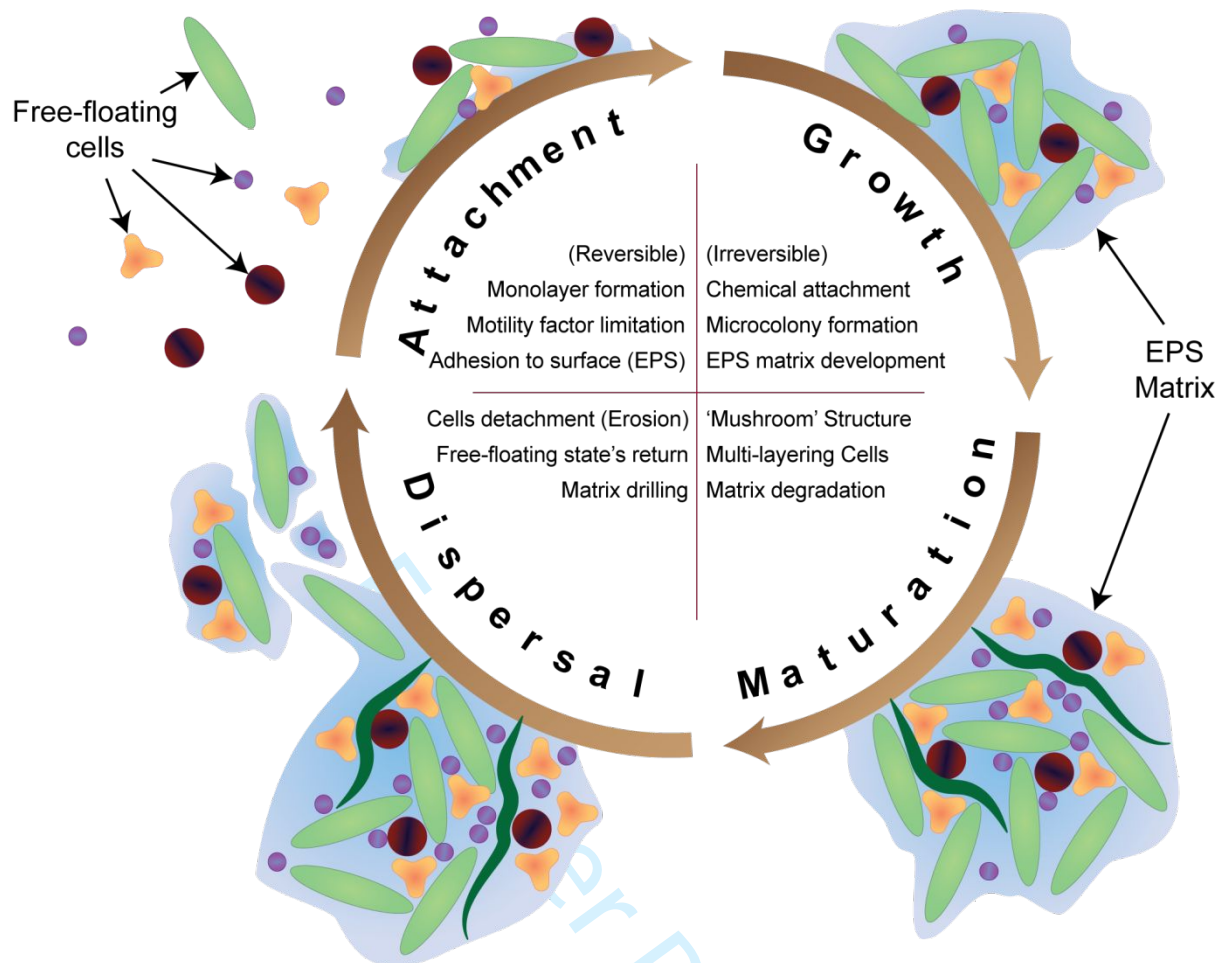
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Figure 1: Biofilm development stages. From planktonic phase, microbes deposit and attach on the surface and start producing extracellular polymeric substances (EPS). With the secretion of EPS substances, the biofilm enters its growth stage and microcolonies are formed. When the biofilm matures, it may reach a 'mushroom' structure where slough of biofilm will later be affected by erosion forces and dispersal. This dispersal stage will link together local communities and form biofilm metacommunities.

3.2 Biostabilization of sediments by biofilms

The hypothesis that biofilms cause biostabilization was suggested early in the 1930s by Carter (1932; 1933a; 1933b), but it was only quantitatively confirmed in the 1970s (Neumann *et al.*, 1970; Scoffin, 1970; Holland *et al.*, 1974). Traditionally, sediment transport has been seen as a physical process (Le Hir *et al.*, 2007), related to channel hydraulics (e.g., Shields, 1936). However, in natural ecosystems, sediment transport processes can be altered by biotic influences (Flemming, 2002). This process is known as 'biostabilization', where organisms decrease the susceptibility of sediment to erosion (Paterson and Daborn, 1991).

Particle movement in streams starts when bed shear stress τ_o exceeds a certain threshold, the critical bed shear stress τ_{oc} (e.g., Leopold *et al.*, 1964; Richards, 1982; Fang *et al.*, 2014). It is now recognized that biofilms tend to increase τ_{oc} (Neumeier *et al.*, 2006; Fang *et al.*, 2014; Pivato *et al.*, 2019). EPSs are the major driver of increased cohesion and stability of sediments (de Boer, 1981; Grant and Gust, 1987; Paterson, 1989; 1994; Dade *et al.*, 1990). Following Tolhurst *et al.* (2002), EPSs involve sediment stabilization by either

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222 physical binding (apparent cohesion) or molecular electrochemical interactions (chemical
223 cohesion).
224
225 It is also known that the biofilms modify bed morphology, so changing bed roughness,
226 influencing near-bed velocities and ultimately impacting sediment transport (van Rijn, 2007).
227 Biofilms may themselves have a morphology and, as a result, they may increase (Flemming
228 *et al*., 2007a) or reduce (Fang *et al*., 2014) bed roughness. Biofilms can increase the
229 roughness by developing free-flowing "fluffy" morphologies (e.g., free flowing streamers) that
230 are easily erodible along with the uppermost sediment layers even at low flows (Flemming *et*
231 *al*., 2007a). On the other hand, biofilms can also reduce bed roughness by developing
232 smoother mats, which reduce the shear stress available to transport the particles (Fang *et*
233 *al*., 2014). However, this can also reduce the energy losses at the surface, change shear
234 stress partitioning and ultimately increase the component of shear stress available to entrain
235 and transport sediment. Bed-smoothing (e.g., by introduction of finer sediments) has been
236 shown to lead to bed destabilization (Wilcock *et al*., 2001; An *et al*., 2019) independent of
237 any increases in critical shear stress. Whilst biofilms may increase resistance to motion, their
238 impact on shear stress partitioning may also increase the shear stress available for
239 transport, which results in an increase of the susceptibility of the bed to being eroded. Thus,
240 the bed stabilization provided by biofilms is a function of the balance between the forces that
241 increase sediment cohesion and hence resistance to erosion and the forces that tend to
242 erode them, both external (e.g., shear stress) and internal to the biofilms (e.g., fluffy
243 morphologies, smoothed mats).
244
245 Whether or not biofilms stabilize sediments, it appears that this process is particle size
246 dependent, and proportionally more important for finer particles. For instance, Statzner *et al*.
247 (1999) found that benthic microalgae and their biofilms are able to stabilize sand particles,
248 i.e. those finer than 2 mm. The fact that biofilm stabilization is potentially particle size
249 dependent, and greater for finer sediments, perhaps explains why there has been more
250 focus on marine environments (e.g., tidal flats) than on freshwater environments (Fang *et al*.,
251 2014). Freshwater environments can have coarser bed sediment but many coastal
252 environments are depositional, composed of terrestrially-derived material that has been
253 sorted by rivers and streams, such that most material is finer.
254
255 Biostabilization also appears to be more efficient in saltwater than in freshwater because of
256 ion concentrations related to seawater chemical properties (Spears *et al*., 2008; Gerbersdorf
257 and Wieprecht, 2015). It has been shown (Flemming and Wingender, 2010) that
258 biostabilization could be enhanced by a surplus of cations, such as in saltwater, that helps to
259 create strong electrochemical bridges between the EPS and the sediments. For instance,
260 Stal (2003) and Flemming *et al*. (2007a) found that an increase in Ca^{2+} (and in general of all
261 divalent cations) has the consequence of increasing the binding forces between the matrix
262 and the sediments resulting in greater biostabilization.
263
264 To investigate the role of biofilms in stabilizing sediments, the analysis of shear stress and/or
265 critical shear stress is common. Grant and Gust (1987) investigated the role of purple
266 sulphur bacterial mats in stabilizing marine sediments, and they tested their hypothesis in
267 laboratory flumes with samples collected directly on a South Florida beach. By increasing
268 flume discharge (i.e., increasing τ_o) until the erosion threshold was reached, they

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269 demonstrated that colonized sediments have a τ_{oc} up to five times higher compared with
270 sterile sediments (Grant and Gust, 1987). Similar results were recorded by Tolhurst *et al*.
271 (2002) who found a 3.7 times increase in τ_{oc}. In their experiments, they used cohesive
272 sediments from a Scottish estuary and a variable amount of commercially extracted EPSs
273 (Tolhurst *et al*., 2002), which mimics the natural increase of EPSs following biofilm growth
274 but without the need to wait for natural biofilm growth.

275

276 Neumeier *et al*. (2006) simulated diatom biofilm growth for a tidal environment in a laboratory
277 flume in a 28-day experiment. They reported a 10 fold increase in τ_{oc} for sediments
278 colonized by a well-developed biofilm (after 28 days of colonization) compared with abiotic
279 sediments (Neumeier *et al*., 2006). In two 5-week experiments using small glass beads and
280 biofilms sampled in a Scottish estuary, Gerbersdorf *et al*. (2008b) and Gerbersdorf *et al*.
281 (2009) found that τ_{oc} was up to 3.6 and 10.8 times higher respectively compared with abiotic
282 controls. The difference between these two increases was explained by the use of bacteria
283 only in the former experiment and by the use of a mixture of bacteria and diatoms in the
284 latter experiment (Gerbersdorf *et al*., 2009). Gerbersdorf *et al*. (2009) stated that one
285 possible reason for this increase was synergistic interactions between diatoms and bacteria,
286 with the former profiting from the exudates of the latter and *vice versa*.

287

288 Vignaga (2012) investigated biostabilization by freshwater cyanobacteria using experimental
289 flumes, different particle sizes (1 mm, 1.2 mm and 2.2 mm) and different growth periods (up
290 to 10 weeks of colonization). Results showed the greatest biostabilization after 4 weeks with
291 a maximum increase of τ_{oc} of 43% for particles of 1 mm, 35% for particles of 2.2 mm and
292 30% for particles of 1.2 mm (Vignaga, 2012). This confirms the above-mentioned hypothesis
293 that the impact of biofilms is likely to be greater for finer sediment. Thom *et al*. (2015), in 4-
294 to 8-week experiments using flumes, riverine water, and glass beads of 0.1 and 0.2 mm
295 showed a maximum increase of stability of almost 10 times compared with an abiotic
296 reference (τ_{oc} = 0.23 Nm^{-2}) (Thom *et al*., 2015).

297

298 Thom *et al*. (2015) also found that biostabilization is a seasonally driven phenomenon; the
299 increase of τ_{oc} changes through the year. Sediment stability was just 1 to 1.5 times τ_{oc} for
300 late autumn conditions, 3 times τ_{oc} for summer conditions and at maximum (10 times) for
301 spring conditions (Thom *et al*., 2015). Schmidt *et al*. (2016) also found a maximum increase
302 of sediment stability with spring conditions and a minimum with autumn conditions.
303 Seasonality has also been recorded in tidal environments (e.g., Widdows *et al*., 2000; Amos
304 *et al*., 2004).
305 Pivato *et al*. (2019) showed that during winter and early spring biofilm growth was limited by
306 low sediment temperatures and light availability. The low growth rate results in less
307 developed winter biofilms (low biomass) incapable of stabilizing sediment because the mat
308 was not developed enough to significantly increase the shear stress (Pivato *et al*., 2019).
309 However, when meteorological and environmental conditions (e.g., light availability and
310 sediment temperature) were suitable, the biofilm was able to mature rapidly and to provide
311 effective biostabilization because the mat was developed enough to support higher shear
312 stress (Pivato *et al*., 2019).

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314   Other studies have considered the role of disturbance, here referred as an increase in the
315   shear stress that could lead to bed destabilization and subsequent biofilm detachment, in
316   conditioning how biofilms influence biostabilization. Mariotti and Fagherazzi (2012) modeled
317   biofilms impacts under different disturbance scenarios in tidal environments. In their first
318   scenario, strong but infrequent disturbances were applied to the biofilm, in the second, weak
319   and infrequent disturbances were applied, while in the third weak (of the same magnitude of
320   scenario 2) weak and frequent disturbances were applied. In the first case, biofilm biomass
321   and τ_{oc} increased until the occurrence of the disturbance, which systematically destroyed the
322   biofilm and re-started the cycle. In the second case, disturbances were neither large enough
323   nor frequent enough to have a negative impact on the biofilm, which increased in both
324   biomass and τ_{oc} until an equilibrium state was reached, defined here as the point in which
325   biomass and critical shear stress values fluctuate around a steady mean value. In the third
326   case, frequent weak disturbances destroyed the biofilm progressively. From the last two
327   scenarios, it appears that biofilm biostabilization is also a function of biofilm growth history
328   (Mariotti and Fagherazzi, 2012). In similar projects, Yallop *et al*. (1994), Valentine *et al*.
329   (2014) and Chen *et al*. (2017; 2019) for tidal environments and Thom *et al*. (2015) for
330   riverine systems found that shorter growth periods lead to reduced stabilization effects,
331   whilst long periods allow for stronger stability resulting in an increased ability to support
332   greater shear stresses.

334   Chen *et al*. (2017) proposed also that the role of EPSs in stabilizing sediment is not only a
335   surficial phenomenon, and they argued that EPSs can penetrate into sediment beds allowing
336   for a deeper impact of biostabilization. In fact, they showed that after the failure of the
337   surficial biofilm layer, the sediment stability still remained in place (Chen *et al*., 2017).

339   In summary, biofilms have the capacity to increase the critical shear stress of sediments, in
340   particular by producing viscoelastic EPSs. With increasing biostabilization, biofilms construct
341   their own niche and enhance the habitability of an otherwise unstable sedimentary
342   environment. With better habitability, biofilms proliferate resulting in greater EPS production
343   and increased sediment stability, and so on until they are scoured or disintegrate. Hence, by
344   changing the sediment state from unconsolidated to consolidated, biofilms act as allogenic
345   engineers and this is done intentionally. Therefore, we propose the biostabilization of
346   sedimentary environments as another important emergent property of the biofilm mode of life
347   in streams, but whose importance is likely to be context specific (e.g., more important for fine
348   sediments than coarse sediments).

3.3 Fertilization of sediments by biofilms

351   The mineral surfaces of stream sediments are typically devoid of significant amounts of
352   organic substances. Dissolved molecules can sorb to the mineral surfaces thereby forming
353   organomineral complexes (Aufdenkampe *et al*., 2011), which are typically thought to be
354   protected from metabolism and hence of minor relevance for ecological processes (Rothman
355   and Forney, 2007). As microbial biofilms colonize and accumulate on these mineral
356   surfaces, they change the chemical stoichiometry of the sedimentary environment. Several
357   processes are involved in this chemical shift. The adhesion of bacterial cells to minerals
358   enriches their surface in nitrogen (N) and phosphorus (P) relative to carbon (C). This is
359   because the C:N and C:P ratio of bacterial cells typically varies from 4 to 8 and 10 to 80,

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respectively (Hall *et al.*, 2010). Microbial in origin, EPS are biopolymers that not only contain polysaccharides, but also DNA and a large variety of proteins as well (Flemming *et al.*, 2007b). As cells start proliferating and producing EPS they add organic carbon to the mineral matrix. Depending on the contribution of extracellular DNA and proteins to the EPS, the build-up of a biofilm matrix further enriches the mineral environment in P and N. As cells decay within the biofilms, their organic constituents are released to the matrix where they are transiently protected from loss through water flow, for instance. The exudation of storage compounds by algae to maintain stoichiometric homeostasis during peak photosynthesis or shortly thereafter further contributes to chemical enrichment with the biofilm matrix. It is the close spatial proximity between the transient storage of reactive solutes and active cells that facilitates the remineralisation and elemental cycling within biofilms (Battin *et al.*, 2003). At the same time, the EPS matrix easily scavenges solutes from the streamwater owing to its very large surface area and chemical surface properties (Freeman and Lock, 1995; Flemming *et al.*, 2016). As the biofilm matrix is enriched by EPS secretion and other chemical processes, more dissolved molecules sorb on mineral surfaces. This process is thus claimed to fertilize the biofilm's surrounding environment (Flemming and Wingender, 2010).

We argue therefore that the enrichment in nutrients by microorganisms and aided by the biofilm matrix acts as a fertilizer of an otherwise nutrient-poor mineral matrix. This is analogous to the soil build-up during primary vegetation succession. In streams, this process may gain relevance with concomitant biostabilization. In fact, it would be the latter that provides a time scale for microbial biofilms to accumulate and to recycle nutrients, and thereby fertilize the sediments. This is why we propose that biofilms act as allogenic engineers that alter the environment through material transformation (Jones *et al.*, 1994). The resources resulting from this engineering become available for other microorganisms, but also for macroinvertebrates and potentially for plant seedlings as well. Fertilization can be understood as an intentional engineering process with a positive feedback on all microorganisms composing the biofilm matrix. In fact, nutrient enrichment within the sedimentary environment facilitates biofilm proliferation and further enhances nutrient stripping from the streamwater.

Key definitions:

Autogenic: autogenic engineers are organisms that change their surrounding environment through their own living or dead tissues, such as vegetation that increases river bank stability through its own biological structure.

Allogenic: allogenic engineers are organisms that change their surrounding environment through the transformation of materials from one state to another, such as beavers that build wooden dams by cutting living trees.

Intentional engineering: intentional modification of the surrounding environment to benefit from it (e.g., nest digging by salmonids).

Unintentional engineering: unintentional modification of the surrounding environment that does not provide direct feedbacks to the engineer, but it can have positive or negative impacts upon other organisms.

Extracellular Polymeric Substances (EPSs): biomolecules binding cells to each other and to solid materials mainly composed of polysaccharides and proteins.

Prokaryotes: Unicellular organisms lacking internal membrane-bound structure without a distinct nucleus.

Lysed cells: Cells affected by the breakdown of membrane due to virial, enzymatic or osmotic processes compromising its integrity.

Stoichiometric homeostasis: property of an organism to keep its biomass element ratio relatively stable independently of its substrate.

Roughness: roughness describes the loss of energy experienced by the flowing water due to the friction against the streambed and/or banks. Related to channel morphology (e.g., grain size, grain angle, etc.), it influences hydraulic components such as flow velocities, turbulence and particle motion, as well as the ecological setting of the benthic substratum.

Critical shear stress: the critical shear stress (τ_{oc}) is the threshold from which particles can be mobilized. Below this threshold, resisting forces (e.g. gravity) keep grains on the streambed; above this threshold, moving forces initiate particle movement. Hence, particle movement begins only when the shear stress (τ_o) exerted by water on the grains is greater than the critical shear stress defined by properties of the streambed.

Ontogeny: in biology, ontogeny refers to development of an organism, an anatomical part or a behavioral trait through time. In this paper, we refer to the ecological development of glacial floodplains. In particular, we refer to the way in which life develops in these environments by converting barren, hostile and water-limited soils to fertile and water retaining ones (i.e., morphogenesis of a rocky environment).

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4. Biofilms, ecosystem engineering and the ontogeny of glacial floodplains

4.1 Glacial floodplains and streams: highly dynamic environments

Glacial floodplains are highly dynamic environments experiencing continuous morphological change (Marren, 2005; Heckmann *et al.*, 2016). Stream braiding is common in these environments (Maizels, 1995; Marren, 2005), and is controlled by both allogenic and autogenic factors (Ashworth and Ferguson, 1986). The system is externally influenced by discharge and sediment delivery. These combine with the extant morphology to determine spatial patterns of flow velocity and shear stress, as well as the sediment available for transport (Ashworth and Ferguson, 1986). Internally, shear stress partitioning and sediment availability regulate sediment transport. The latter shape channel morphology; and may sort sediment on the streambed, so changing bed roughness and velocity distributions and consequently the shear stresses (Ashworth and Ferguson, 1986). Bed sediment sorting will also change τ_{oc}. Thus, external factors control the internal ones and *vice versa*.

Discharge in glaciated river basins, and consequently in glacial forefields, has substantial variations both daily and yearly (Maizels, 1995; Marren, 2005), and it is usually charged with sediment in the form of bedload or suspended load (Gurnell, 1987; Milner and Petts, 1994). Daily or diurnal flow changes interact with stream bathymetry to drive rapid increases and then decreases in bed shear stress and hence sediment supply and sediment transport. Runoff can be produced by snowmelt or ice melt. Because the majority of ice melt is produced at the glacier surface (Nienow *et al.*, 1998), ice melt is driven primarily by solar radiation, temperature and wind speed (see Fountain, 1996; Nienow *et al.*, 1998; Swift *et al.*, 2005). Annually, discharge is strongly bound with radiation and temperature variations (Maizels, 1995; Lane and Nienow, 2019). Discharge is low in winter (Maizels, 1995; Malard *et al.*, 1999) because the air temperature is below the melting point of ice. During late spring and summer, solar radiation becomes more intense and temperatures rise, and the daily flow maxima and variability increase due to snowpack melt (Nienow et al., 1998). As snow cover tends both to slow melt and to buffer melt water delivery to the stream, as long as the basin remains significantly snow covered, flow maxima tend to be damped and baseflows maintained (Lane and Nienow, 2019). However, as snow melt occurs and the snow line retreats up a glacier, ice melt begins. As ice has a lower albedo than snow, melt rates are higher and as ice has a much lower porosity that snow, buffering and hence flow attenuation are reduced. Thus, peak flows become bigger and baseflows become smaller (Nienow *et al.*, 1998; Malard *et* al., 1999; Swift *et al.*, 2005; Lane and Nienow, 2019) through the melt season. By the end of the summer, falling incoming solar radiation causes glacier melt and so peak discharge to decrease but diurnal discharge variation is maintained. By late autumn, discharge approaches the winter minima (Maizels, 1995).

This variability in discharge is also coupled to strong variability in both suspended load and bedload. In glacial forefields, sediment sources may be either glacial or periglacial. The latter can be important, although this does depend on the degree of valley sidewall to proglacial stream coupling, which may be limited by alluvial fan formation (Lane *et al.*, 2017). Over annual to decadal time-scales glacial sediment sources are predominantly related to subglacial sediment evacuation by glacier melt. Measurements close to glacier margins (Mao *et al.*, 2019) show distinct timescales of variation in suspended sediment concentration

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(SSC)-discharge relations. At the daily time-scale (Clifford *et al*., 1995; Perolo *et al*., 2019), clockwise hysteresis can result because discharge forces shear stress to rise above the critical value needed for bed sediment transport and subglacial bed-accumulated fines are released. These become exhausted during the day, leading to lower concentrations on the falling limb. Superimposed on such daily time-scales there may be a seasonal evolution. As sediment evacuation from glaciers falls to almost zero through winter, but at least some glacial erosion (due to ice deformation) may continue, there may be subglacial sediment accumulation during winter and early spring. This is evacuated and progressively exhausted through the melt season such that the degree of daily clockwise hysteresis may reduce (Clifford *et al*., 1995; Hodgkins, 1996; Riihimaki *et al*., 2005; Stott *et al*., 2014; Mao and Carrillo, 2017). It may also reduce due to the development of more channelized subglacial streams which reduce meltwater access to the bed of the glacier where sediment has accumulated and hence reduces sediment supply (Nienow *et al*., 1998; Mair *et al*., 2002; Swift *et al*., 2002; Kulessa *et al*., 2008; Gimbert *et al*., 2016).

Bedload is more difficult to measure and so it is less well known (Mao *et al*., 2019). Glacial streams are thought to be bedload dominated (Alley *et al*., 1997). Evidence points to some similarities with suspended sediment dynamics. Bedload transport appears to be controlled by discharge magnitude and variability. Perolo *et al*. (2019) showed how late season bedload export from an Alpine valley glacier switched on during the day and off during the night in response to variation in discharge and hence shear stress, leading to clockwise bedload transport hysteresis at the daily time-scale. Using a hydraulic model for the whole melt season, they showed that bedload transport capacity was higher when the intensity of diurnal discharge fluctuation was greater because bedload responded as a non-linear function of discharge over a critical value. Such changes in capacity may not be reflected in actual transport because, as with suspended sediment, there may be exhaustion effects at both the daily timescale but also at the seasonal timescale. However, such processes have rarely been studied.

The regular rise and fall of stream discharge, and hence bed shear stress, results in rates of morphodynamic change that are elevated as compared with non-glacial streams. Provided there is enough lateral accommodation space, high rates of sediment supply coupled to discharges that frequently exceed the threshold at which sediments start to move, lead to braided channel patterns. This may be reinforced by relatively low rates of ecosystem engineering due to vegetation, given climate conditions. Channel reworking rates have been shown to be a function of combined discharge and sediment supply variability (Lane *et al*., 1996) and give rise to a complex template of channels, submerged bedforms and exposed gravel bars (Germanoski and Schumm, 1993). Due to data collection challenges there are no studies that have quantified reworking rates at high frequency over an entire melt season. Bakker *et al*. (2019) presented data for a three week period, calculating bedload transport from measured erosion and deposition patterns. Figure 2 shows how bedload transport (and hence erosion and deposition) occurs over a number of different time-scales and that during their 3 week study there was no part of the river occupied by water that was not reworked. This is of particular importance for biofilm development as rates of disturbance are so high that it is only likely to be in the early and late summer, when channel reworking rates fall, that there will be enough stability for biofilm development.
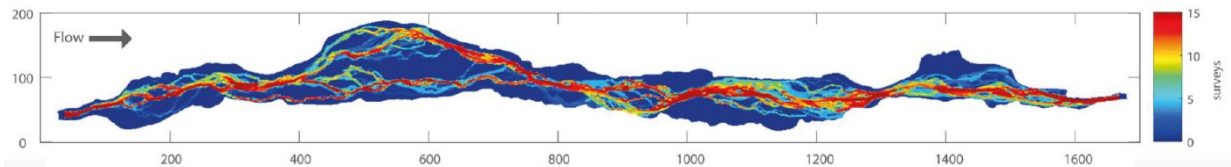
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526
527 Figure 2: Transport frequency in an Alpine braided system showing the frequency of disturbances for
528 15 surveys of a river over a 21-day period (after Bakker et al., 2019). The x- and y-scales are given in
529 meters.

530 Away from the morphodynamically active zone, zones that were previously active may
531 become stable and allow vegetation succession (Figure 3). These are commonly on
532 terraces, where incision of the active zone has reduced inundation and hence sediment
533 transport and channel change frequency (Thompson and Jones, 1986; Thompson, 1988;
534 Germanosky and Schumm, 1993; Marren, 2002; Marren and Toomath, 2013; 2014; Roussel
535 et al., 2018). Terrace formation depends upon the balance between sediment supply and
536 sediment transport capacity (and hence glacier melt). With glacier recession, there is
537 evidence (de Winter et al., 2012; Cordier et al., 2017; Roussel et al., 2018) that sediment
538 supply does not keep up with capacity. The result is typically incision in front of retreating
539 glacier margins, which provides sediment necessary for downstream aggradation (incision-
540 aggradation, Marren, 2002; Beylich et al., 2009; Marren and Toomath, 2014; Roussel et al.,
541 2018), although the extent to which this happens depends on valley slope and on whether or
542 not proglacial lakes form that can disconnect downstream sediment delivery (Bogen et al.,
543 2015). But, conditions have been observed where supply can keep up with capacity
544 increases and aggradation is observed throughout the forefield (Curran et al., 2017). In
545 flume experiments, Germanoski and Schumm (1993) showed that channel patterns
546 associated with incision-aggradation are nearly always braided in aggradational zones, but
547 may be braided or straight in incision zones, depending on incision rate; incising reaches
548 invariably produce terraces, but higher incision rates are needed for a straight channel.

549
550 Given the apparent importance of more stable zones in supporting biofilm development (see
551 Miller and Lane, 2019 and also Figures 3 and 5), this terrace formation is important.
552 However, it is unlikely to be sufficient for biofilm development and vegetation succession.
553 Glaciogenic deposits are typically extremely well drained and terraces, higher than the
554 morphodynamically active river may be hydrologically stressed. To support ecological
555 processes and succession, including biofilm development, water accessibility remains crucial
556 (Rydgren et al., 2014) which implies that terraces need to be hydrologically connected,
557 whether to surface water or groundwater (see Miller and Lane, 2019). This makes
558 ecosystem processes very dependent upon water sources besides those derived from the
559 morphodynamically active stream itself, especially as incision is likely to have decoupled
560 such terraces from groundwater supply by the mainstream. Such terraces are more likely to
561 be dependent on snow-melt fed or spring-fed streams supplying water from the hillslopes
562 (e.g., Malard et al., 1999; Ward et al., 1999) or larger-scale groundwater transfers. Snow-
563 melt sources also tend to be seasonally-variable (Malard et al., 1999) and evidence (Malard
564 et al., 1999) suggests that in summertime terraces are supported by the hillslope-derived
565 groundwater.
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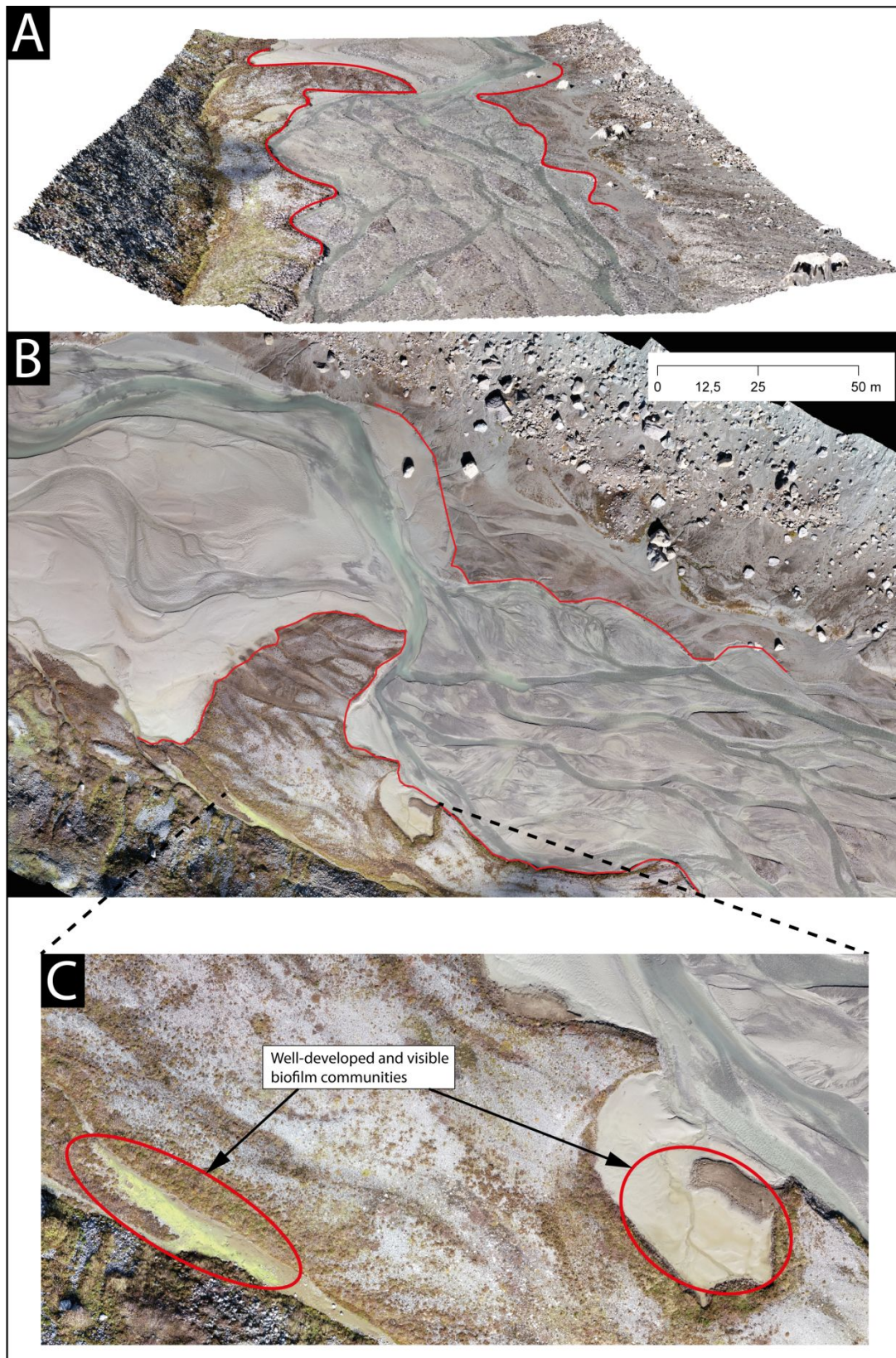
Figure 3: The Valsorey floodplain (Valais, Switzerland) in October 2018. The floodplain shows clearly primary succession patterns, which are confined to terraces (red lines mark the edges) on both sides of the river that are not reworked by the main braidplain (sub-figures A and B). Well-developed and visible biofilm communities tend to be restricted to channels located on terraces (sub-figure C) because disturbances are not too frequent to destroy the mats.

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4.2 Proposed model of biofilms in glacier floodplain ecosystem ontogeny

From theory to reality

Previous sections showed how biofilms can act both as biostabilizators and fertilizers. In an ideal ecosystem, with the absence of abiotic disturbances both fertilization and biostabilization effects will increase with time (Figure 4A). The more stable the sediments are, the more biofilms will expand, grow and stabilize (Figure 1), and the more these effects will extend laterally to surrounding areas. The more nutrients captured within the biofilm matrix, the more enzymes will be produced, biofilm growth enhanced, and fertilization increased. These two processes should be complementary to one another and create a positive feedback loop that represents the first of the two types of ecosystem engineering identified above.

In theory, sediment fertilization allows microorganism and small plants to grow, and roots will enhance the stabilisation of these sediments. Biostabilization should enhance fertilization by making biofilms and sediments less sensitive to erosion and by allowing the biofilm to store nutrients within its matrix and in sediments. This is the second type of bioengineering identified above. However, glacier-fed streams are continuously exposed to high-flow induced disturbances that may counter the potential effects of biostabilization. There are also questions that are yet unresolved regarding the extent to which biostabilization can really increase τ_{oc} sufficiently. The typical magnitude of the increases in τ_{oc} reported for the fine sediments typical of tidal environments are much lower than the magnitudes of the τ_{oc} values reported for the sediments, gravels and coarser (e.g., 100 to 150 Nm^{-2}) typical of glacial floodplain material. Thus, the biostabilization effects may be variable spatially, more important where there is sandy or silty material, which itself is more easily erodible and less likely to be stable.

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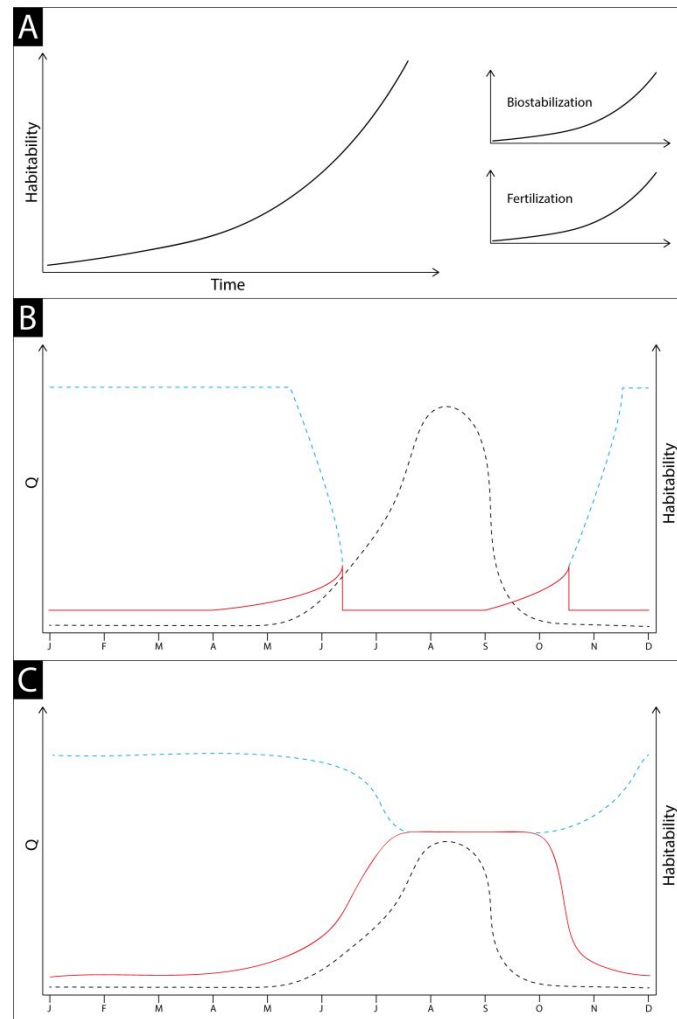
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601 Figure 4: A) Ideal model where disturbances do not occur during biofilm development leading to an
602 exponential increase of habitability; B) Conceptual model of the variation in habitability in relation with
603 stream discharge (Q) in the active floodplain. The black dashed line is the discharge (Q), the solid red
604 line is the habitability, the blue dashed line represents the case in which habitability is increased
605 during the winter time; C) Conceptual model of the variation in habitability in relation with stream
606 discharge (Q) in the abandoned channels.

607 *Active floodplain*

608

609 As highlighted in Section 4.1, stream dynamics continuously shape and re-shape glacial
610 forefields. This reworking may be seasonal, with periods of higher and lower rates of
611 reworking that follow glacial hydrological and sediment supply regimes. Four periods can be
612 identified and related to potential biofilm ecosystem engineering, namely summer, autumn,
613 winter and spring (Figure 4B). These periods don't map onto normal (e.g. astronomical or
614 meteorological) definitions of the seasons and will vary substantially from year to year: for
615 instance, at altitudes of 2000 m or higher, snowmelt in the glacial forefield may start as early
616 as May or as late as early July depending on altitude and orientation (and hence shading);
617 similarly, permanent snowfall in winter may occur as early as late September or as late as
618 early December.

619

620 Summer experiences the highest discharges because of ice melt (Nienow *et al.*, 1998).
621 Additionally, summertime has intense diurnal flow variations (Nienow *et al.*, 1998; Swift *et*
622 *al.*, 2005; Lane and Nienow, 2019). The increase in peak daily discharge and in the intensity
623 of diurnal discharge variation through the melt season, which also drives high rates of
624 sediment delivery (Perolo *et al.*, 2019), leads to the morphodynamically most active period.
625 Not only may such activity erode the sediments to which biofilms are bound, the high
626 sediment transport rate (Milner and Petts, 1994) and flow shear stresses (Cullis *et al.*, 2014)
627 may scour biofilms from bed sediments. Because disturbances are frequent, biofilms cannot
628 fully develop and they cannot impact stream habitability. The time between two subsequent
629 disturbances is too short to allow biofilms to reach a state of maturity (Thom *et al.*, 2015).
630 Thus, during the summer, biofilm development tends to be restricted to morphodynamically
631 inactive zones (e.g., terraces; see below) and then limited by access to other resources,
632 notably water.

633

634 When autumn approaches, from late August onwards, temperatures drop as does the
635 discharge due to reduced melt. Although flow variation is commonly still important (Lane and
636 Nienow, 2019), peak flows are commonly reduced and the rate of morphodynamic change
637 falls. As a result, the size of the morphodynamically active zone contracts (Malard *et al.*,
638 1999). Less-incised channels receive less discharge compared with well-incised ones where
639 the bulk water flows preferentially, resulting in lower shear stress and greater probability that
640 flow depth is less than the euphotic depth and solar radiation can reach the stream bed.
641 Provided such channels are stable, biofilms may develop and increase habitability because
642 irreversible attachment and EPS secretion is possible (Stoodley *et al.*, 2002). Whether or not
643 this has a positive feedback on stability of such streams is not yet known. The increase in
644 habitability continues until the first significant snow which pauses photosynthesis. The latter
645 may also be reduced by the progressive reduction in solar radiation exacerbated in Alpine
646 valley due to relief-driven effects on shading. We know little about how photosynthetic
647 activity evolves as a function of time in such streams during the transition from late summer
648 through autumn to early winter.

649

650 In winter, and even if there are almost no disturbances, we predict that biofilms cannot
651 increase the habitability of the forefields, mainly because of the absence of light, which
652 precludes phototrophic activity. This impedes the provision of energy for other organisms
653 (Lavandier and Décamps, 1984), and given the nutrient depleted nature of glacier forefields
654 (Bardgett and Walker, 2004; Bardgett *et al.*, 2007), there should be few opportunities for
655 chemotrophs to develop. That said, however, some chemotrophic activity could develop
656 during winter if biofilms have accumulated sufficient nutrients in autumn to sustain their
657 metabolic needs when light is no longer available. Coupled with longer periods of stability
658 and appropriate water supply by groundwater (Malard *et al.*, 1999), this should lead biofilms
659 to reach a sufficient state of maturity, able to increase the habitability to its theoretical
660 maximum. This hypothesis is relevant and is one reason why potential consumers of
661 biofilms, such as macroinvertebrate communities, reach their maximum richness during
662 winter in Alpine streams (Gabbud *et al.*, 2019).

663

664 In spring, solar radiation and temperature rise leading to snowmelt. The presence of snow in
665 the basin may attenuate runoff significantly leading to low diurnal flow fluctuations (Lane and
666 Nienow, 2019) with relatively high baseflows. Runoff is typically lower in terms of suspended

20

667 sediment concentrations, until glacier melt starts. Provided discharges are not sufficient
668 enough to cause τ_{oc} to be exceeded, low levels of morphodynamic activity should reduce
669 disturbance which, coupled with high solar radiation intensity once the snowpack
670 disappears, produces ideal conditions for biofilms to increase habitability. We might expect
671 some spatial variability in this process, with the less incised channels being more
672 morphodynamically stable. This "window of opportunity" begins to close as the melt season
673 progresses, diurnal discharge variation becomes more intense, and rates of morphodynamic
674 change increase. Whether or not this increase in habitability has any longer term effect is a
675 moot point as it depends on the extent to which subsequent morphodynamic activity
676 destroys biofilm communities.

677

678 *Lateral gradients*

679

680 As noted above, because of the potential for continuous reworking of the active floodplain, it
681 is the abandoned channels located on terraces where it is most likely that biofilms will lead to
682 a long-term increase in habitability. Such channels are likely to be only very rarely (if ever)
683 inundated by the main stream due to the associated elevation differences. For instance, in
684 the Glacier d'Otemma (Valais, Switzerland), Miller and Lane (2019) found that *c.* 1 m height
685 difference separated the active plain from one terrace on which very developed biofilms
686 were observed (Figure 5) and this surface could not be inundated even at the highest
687 discharges measured. Given their less disturbed nature, abandoned channels on terraces
688 should support biofilm development and so ecosystem engineering (Figures 4C and 5).
689 Moisture cannot be guaranteed, but may be supported by groundwater (Malard *et al.*, 1999),
690 by hillslope-derived flows, or by the positive feedbacks following biofilm development, which
691 reduces vertical infiltration of water (Miller and Lane, 2019).

692

693 In summer water sourced from groundwater and hillslopes will not scour biofilm to a
694 significant degree. Disturbances are small in magnitude and the time between two of them
695 may be long. Hence, biofilms can grow, reach a state of maturity and increase the local
696 habitability to greater levels as compared with the active floodplain. The feedbacks triggered
697 by fertilization and biostabilization can propagate into vegetation succession with evidence
698 that certain plants (i.e. debris vegetation), such as *Saxifraga Aizodes*, *Trifolium Badium, Poa*
699 *Alpina* and *Festuca* Sp., colonize preferentially near channel zones where biofilms create a
700 perched water table (Figure 5B). The only process that can counter this development is
701 lateral erosion of terraces by migration of the morphodynamically active zone.

702

703 In autumn, habitability falls progressively as solar radiation reduces until there is a
704 permanent snow cover and with habitability eventually dropping to winter levels. With the
705 onset of permanent snow cover, the environment should become more suitable for
706 chemotrophs that might profit from nutrients that accumulated before snowfall. During winter,
707 predictions made for the active floodplain should apply to channels located on terraces. In
708 spring, the behavior is similar to that explained in the active floodplain, but the habitability
709 reaches greater levels.

710

711 In summary, as terraces are sites of low disturbance magnitude and frequency, they may
712 allow for ecosystem engineering by biofilms provided that there is sufficient moisture
713 available, commonly related to non-glacial runoff and groundwater. Here we have identified

21

714   an important additional engineering effect of biofilms in glacial floodplains, which is the effect
715   of biofilms on drainage (Figure 5B), crucially important for vegetation establishment
716   (Rydgren *et al.*, 2014) given the ease of drainage of glaciogenic sediments. In that sense, it
717   is plausible that after glacier recession (the surfaces of Figure 5 were still covered by ice in
718   the mid 1990s) and terrace formation, biofilms have played a crucial role in maintaining
719   water at the surface and allowing vegetation to develop progressively in the years after
720   terrace formation. This is of particular interest given that pioneering vegetation has not been
721   able to develop in other proximal zones of the Otemma forefield over the last 30 years, and it
722   has been shown (e.g., Burga *et al.*, 2010) that the first plants can appear as few as ten years
723   after deglaciation. Indeed, it is possible that the effects of biofilms on drainage may be
724   significantly greater than the effects of biofilms on stabilization of sediment, given the size of
725   the glaciogenic sediments that have to be stabilized. These observations emphasize a need
726   to test hypotheses regarding biostabilization and drainage impacts of biofilms in glacial
727   environments, and to include studies of groundwater in such analyses.

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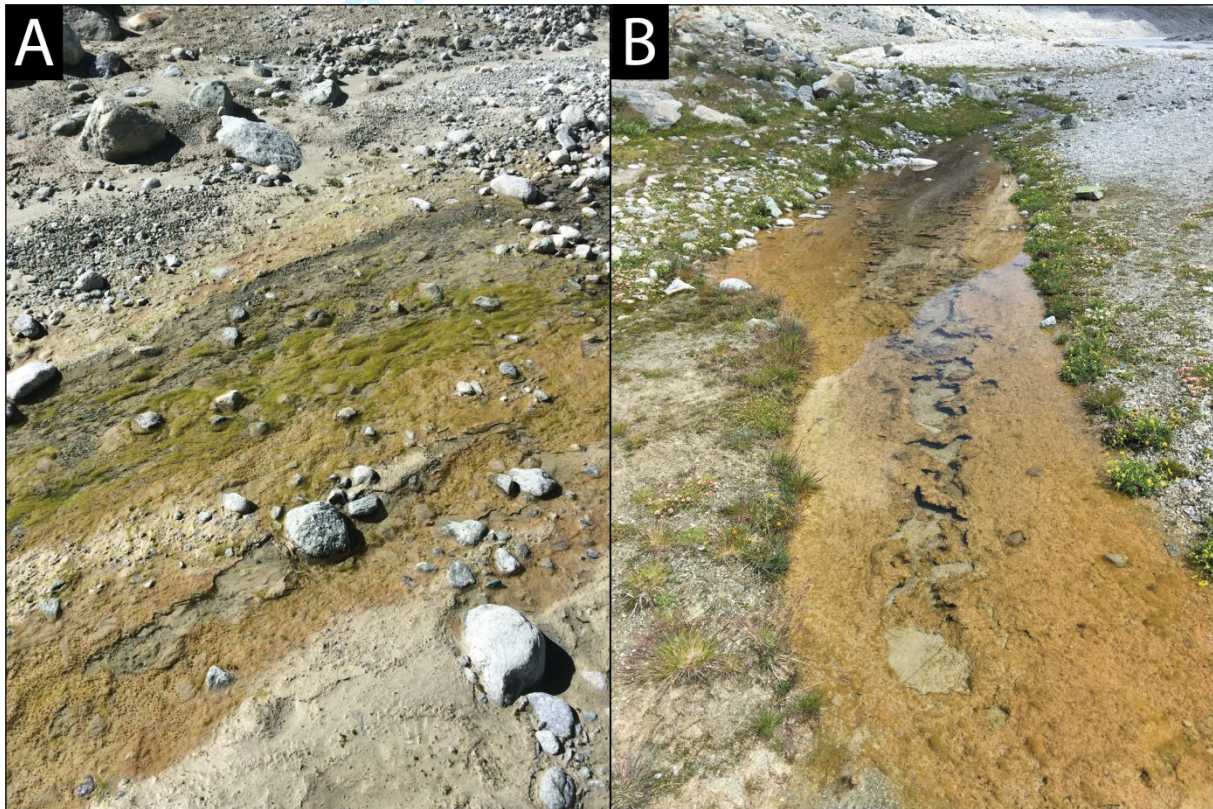
Figure 5: A) Biofilm formation in a stream on a terrace in the Val d'Otemma, Valais, Switzerland; B) A
biofilm mat that has formed in a stream in the Val d'Otemma supplied with hillslope-sourced
groundwater showing successional colonization of the channel margin by vegetation. The stream is
on a terrace about 1 m above the morphodynamically active channel. Note to the right there are
stable bar surfaces, also on the terrace, but largely void of primary production due to severe moisture
limitations related to well-drained glaciogenic sediments.

736   *Longitudinal effects*

737

738   These latitudinal effects need to be put into context. The glacial signals of colder water,
739   discharge variation and sediment supply will all attenuate with distance downstream from a

22

740 glacier (e.g., Milner and Petts, 1994; Füreder, 1999; Burgherr *et al*., 2002; Uehlinger *et al*.,
741 2003). Thus, there is likely to be a progressive reduction in the constraints on biofilm
742 development that results in enhanced biofilm presence, greater rates of biofilm development
743 and increasing habitability. This has been demonstrated for macroinvertebrates by showing
744 that moving away from the glacier snout (i.e. downstream) results in the increase of species
745 richness and diversity (Finn *et al*., 2010).

747 We might conceptualize this as some kind of cusp model: as these constraints reduce
748 downstream, there may be some sort of threshold at which the positive feedbacks that follow
749 from biofilm development become sufficiently strong that they can support vegetation
750 succession. The ecosystem engineering effects that then follow from this succession then
751 start to create more stable zones, more capable of retaining water, where biofilm-driven
752 habitability can increase further.

753 *How can biofilm promote the ontogeny of glacial floodplains?*

755 The above model suggests a need to think critically about the idea that biofilms are simple
756 agents of habitability in glacial floodplains. As discussed above, there is no evidence of an
757 exponential growth in habitability with time. At the same time, there is no evidence to believe
758 that in the active floodplain biofilms can develop enough to promote habitability. By contrast,
759 it appears that in abandoned and less disturbed channels, notably on terraces, the
760 habitability can increase to a favorable point, which means that biofilms can grow up and
761 increase their ecosystem engineering effects. Visual observations (see Figures 3C and 5)
762 and research (Miller and Lane, 2019) confirm that vegetation develops along channels. One
763 might think that this is a result of the presence of flowing water. However, we argue that this
764 view might be limited by the nature of these creeks that tend to dry out gradually during the
765 summer (e.g., Malard *et al*., 1999), both by infiltration and exhaustion of solid water sources
766 (i.e. the snow pack); a phenomenon that should reduce the development of vegetation.
767 Thus, biofilms may be important in determining where vegetation can develop (Figure 5;
768 Miller and Lane, 2019). Additionally, biofilms should increase the amount of soil nutrients
769 available for plants to grow (Kaštovská *et al*., 2005; Schulz *et al*., 2013; Cicazzo *et al*.,
770 2016), which further explains why terraces are not fully covered by vegetation (see the
771 upper-right part of Figure 5B). This effect may be a lateral one related to terraces but also a
772 longitudinal one due to the attenuation described above.

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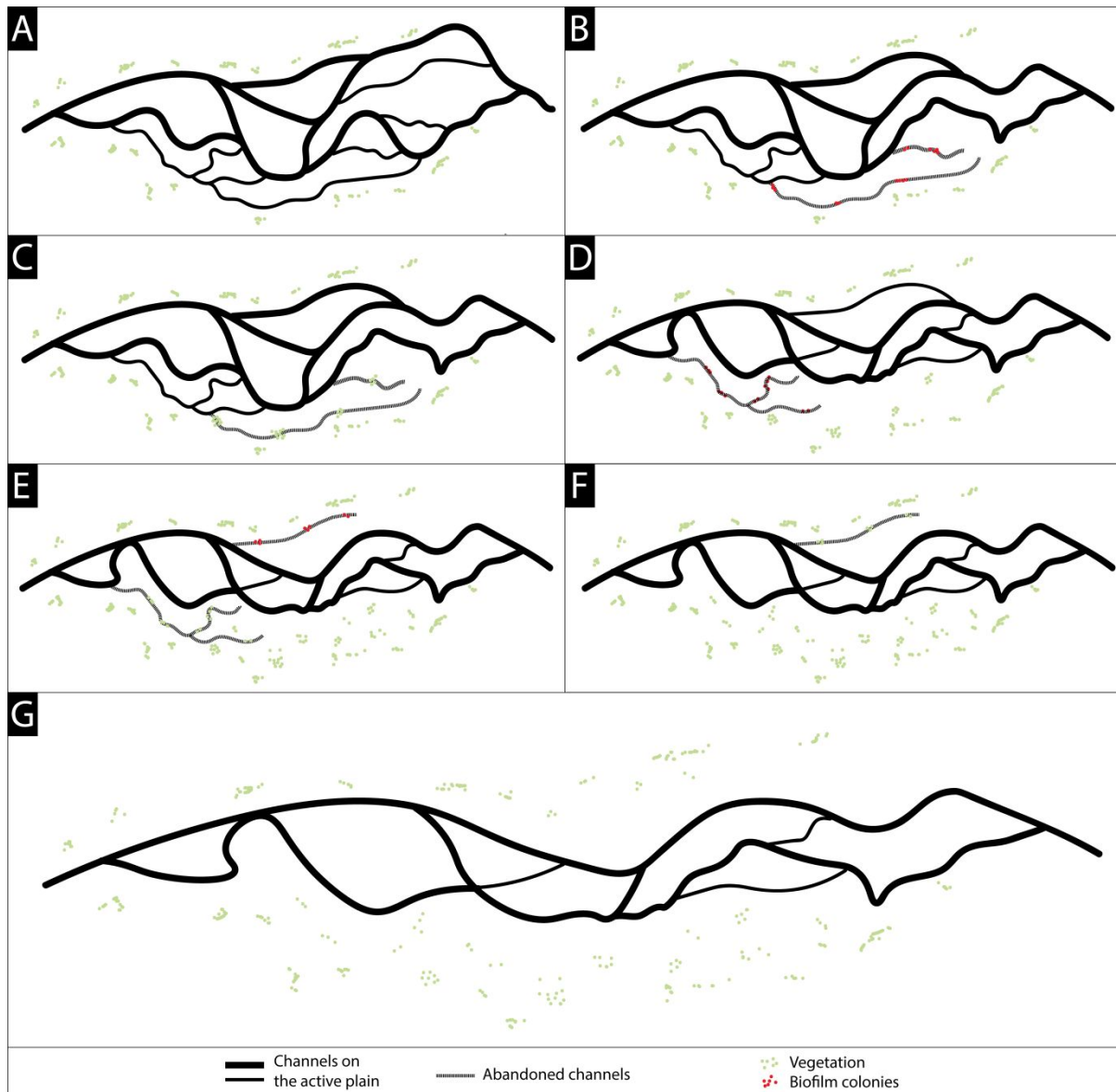
Figure 6: Floodplain ontogeny. A) Floodplain at time t_0 biofilm is no longer developed; B) Floodplain at time t_1 biofilm is developing and coalescing in bigger colonies in abandoned channels, commonly on terraces; C) Floodplain at time t_2. There is vegetation where there were biofilms; D) Floodplain at time t_3. Biofilms develop in the new abandoned channels; E) Floodplain at time t_4. New branches are now disconnected; F) Floodplain at time t_5. There is vegetation where were biofilms; G) Floodplain at time t_6. Vegetation has colonized more floodplain space.

Figure 6 proposes a model for the ontogeny of glacial floodplain ecosystems in relation to biofilms. At the very beginning, the floodplain has a fully-developed braided system, where biofilms do not develop because of the high rate of disturbances (Figure 6A). As mentioned above, there could be some biofilm development in less incised channels during autumn and spring, but this phenomenon is ephemeral and systematically reset by stream dynamics in summer.

As the floodplain evolves, some surfaces are eroded and terraces form (e.g., Thompson and Jones, 1986), becoming disconnected from the main active plain (Figure 6B). Because these abandoned channels are no longer heavily perturbed by stream dynamics, biofilms are able

to develop. The water needed to sustain biofilm development is provided mainly by hillslope groundwater (Malard *et al.*, 1999), which is also thermally less variable (Ward, 1994), less turbid and enriched in nutrients (Brown *et al.*, 2007). These conditions allow biofilms to trigger their engineering feedbacks, in which biostabilization increases fertilization, and *vice versa*. These feedbacks drive an increase of the organic matter content of sediments (Miller and Lane, 2019), promoting primary succession (Raab *et al.*, 2012; Cicazzo *et al.*, 2016) (Figure 6C). Additionally, biofilms can also promote moisture retention by reducing the permeability of channel beds (Miller and Lane, 2019; Figure 5), which reduces loss of water through drainage. This is of importance due to the low permeability of glaciogenic sediment (Burga *et al.*, 2010). The additional engineering effect can be important for maintaining soil moisture if groundwater availability is reduced. Hence, by maintaining water at the surface of channels, biofilms can self-sustain their growth but also promote vegetation succession. Such a phenomenon has been recorded in Glacier d'Otemma forefield, where vegetation seems to grow preferentially along the impermeabilized channels (Figure 5B, Miller and Lane, 2019).

As the floodplain evolves, new surfaces are created by terrace formation, which increases the space for biofilm engineering and vegetation development (Figure 6D, E, F). Theoretically, these processes lead to a decrease of the accommodation space of the braided system. Incision will then create new terraces, further reducing the accommodation space for active braiding and leading to the formation of a more straight single channel (Germanosky and Schumm, 1993). This process may be aided by glacier recession which increases the distance available for the attenuation of glacier flow, sediment and temperature signals.

This overall ecological process is triggered because microbial biofilms not only have the ability to uptake nutrients but also to store them within the biofilm matrix. Overtime, these available nutrients will also be stored in the surrounding soil environment (Kaštovská *et al.*, 2005; Schmidt *et al.*, 2008; Schulz *et al.*, 2013), leading to an enrichment of soil with phosphorous, carbon and nitrogen. Soil enrichment may take some time to occur (already in the first 4 years after deglaciation; Schmidt *et al.*, 2008), however it is a crucial step for glacier floodplain fertilization and succession. By adding nutrients to the soil, biofilms modify soil nutrient content allowing successional processes (Kaštovská *et al.*, 2005; Zumsteg *et al.*, 2012; Raab *et al.*, 2012; Frey *et* al., 2013; Miller and Lane, 2019). Again, this process provides positive feedbacks where biofilm growth leads to more nutrient storage in soil, enhanced sediment stabilization and greater moisture retention. With stabilization and soil enrichment, succession and vegetation development will occur (already in the first 10 years after deglaciation; Burga *et al.*, 2010), further reinforcing the stabilization of sediment and biofilm growth. As architects of soils, microbes are responsible for bedrock material weathering, the source of nutrients in vegetation free sites, potential surface biostabilization and important changes in near surface hydrology (Schulz et al., 2013).

As mentioned by Miller and Lane (2019), the roles of biofilms and vegetation should not be seen separately; they must be linked because the former interact with the latter and *vice versa*. Our model predicts that biofilms have a primordial role in fertilizing the substrate of abandoned channels on fluvial terraces, making other resources (notably water) available and possibly stabilizing sediment. As vegetation develops, the system becomes more stable,

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839 as well as more enriched in organic matter. Our model predicts also that the habitability

840 provided   by   biofilms   reduces   as   winter   comes.

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Conclusion

841 This review paper has highlighted how biofilms may engineer the environment through
842 fertilization and biostabilization, and there are no reasons to exclude them from a list of
843 potential ecosystem engineers just because their engineering is not as visible as that of
844 other organisms or because of their relative small size compared with other ecosystem
845 engineers. Furthermore, it has been argued that it is not accurate to evaluate biostabilization
846 without accounting for fertilization, and *vice versa*, because they both interact together; and
847 that the effects of biofilms on the biostabilization of glaciogenic deposits have not been
848 proved. This is particularly important in scientific terms because it brings together scientists
849 from different domains, such as geomorphology, microbiology and geochemistry.
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852 We also proposed a model for glacial floodplain ecosystem ontogeny that accounts for the
853 engineering effects of biofilms by showing that biofilms are a means of promoting ecological
854 succession in abandoned channels. Their pioneering role allows vegetation to install
855 because conditions become less harsh. As a result, vegetation becomes ecologically
856 relevant. For this reason, it is important to look at the entire successional process instead of
857 looking at a single biological community. It is probably better to consider ecological
858 succession as an extended organism; it is not the single organism (e.g., biofilms and
859 vegetation) that can explain why barren soils become prone to life and then colonized, but
860 the organic whole (i.e. extended organism) acting at each stage. Hence, we argue that it can
861 be erroneous to evaluate the process of ecological succession by investigating one single
862 stage or one single community, because each stage relies on the previous one and each
863 community has synergies with another, and so on. This is the reason why the role of biofilms
864 in ecological succession in deglaciated terrain should be considered as an extended
865 ecosystem engineer that modifies the environment with the ultimate goal to transform it from
866 a hostile one to a livable one.
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868 That said, this model raises a number of questions that need to be investigated. First, we
869 know very little about the biostabilization effects of biofilms in these kinds of environments.
870 Second, we need to consider the timescales of ecosystem succession in relation to the
871 timescales of biofilm development and their engineering effects. Third, we need to validate
872 the latitudinal and longitudinal impacts of biofilms and how these influence ecosystem
873 succession holistically over decadal timescales. Fourth, we need to consider whether
874 vegetation can develop without biofilm engineering in these environments. Finally, we need
875 to look at biofilms at the annual timescale and not just the spring or summer timescale. We
876 need to understand what happens under snow to habitability, for instance. We need to
877 monitor stream morphodynamics continually in parallel with the continuous monitoring of
878 biofilm development and their ecosystem engineering functions. Through such intensive
879 study, we may develop a much better understanding of the ecosystem engineering of
880 biofilms in glacier floodplain ecosystems.

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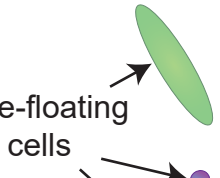Zika, U., & Peter, A. (2002). The introduction of woody debris into a channelized stream:

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2 Free-floating
cells
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Attachment

Growth

(Reversible) | (Irreversible)
Monolayer formation | Chemical attachment
Motility factor limitation | Microcolony formation
Adhesion to surface (EPS) | EPS matrix development

Cells detachment (Erosion) | 'Mushroom' Structure
Free-floating state's return | Multi-layering Cells
Matrix drilling | Matrix degradation

Dispersal

Maturation

EPS Matrix

The Valsorey floodplain (Valais, Switzerland) in October 2018. The floodplain shows clearly primary succession patterns, which are confined to terraces (red lines mark the edges) on both sides of the river that are not reworked by the main braidplain (sub-figures A and B). Well-developed and visible biofilm communities tend to be restricted to channels located on terraces (sub-figure C) because disturbances are not too frequent to destroy the mats.
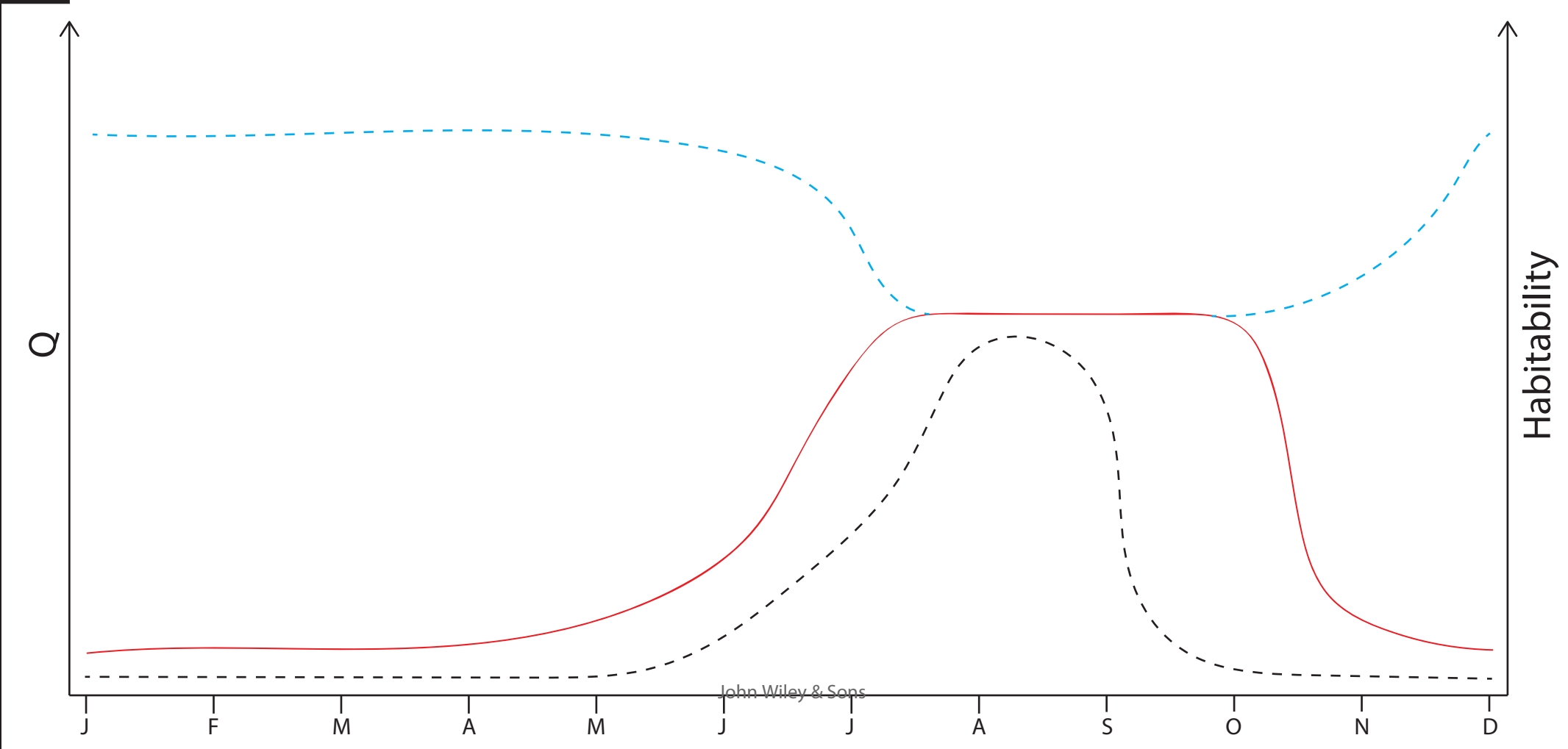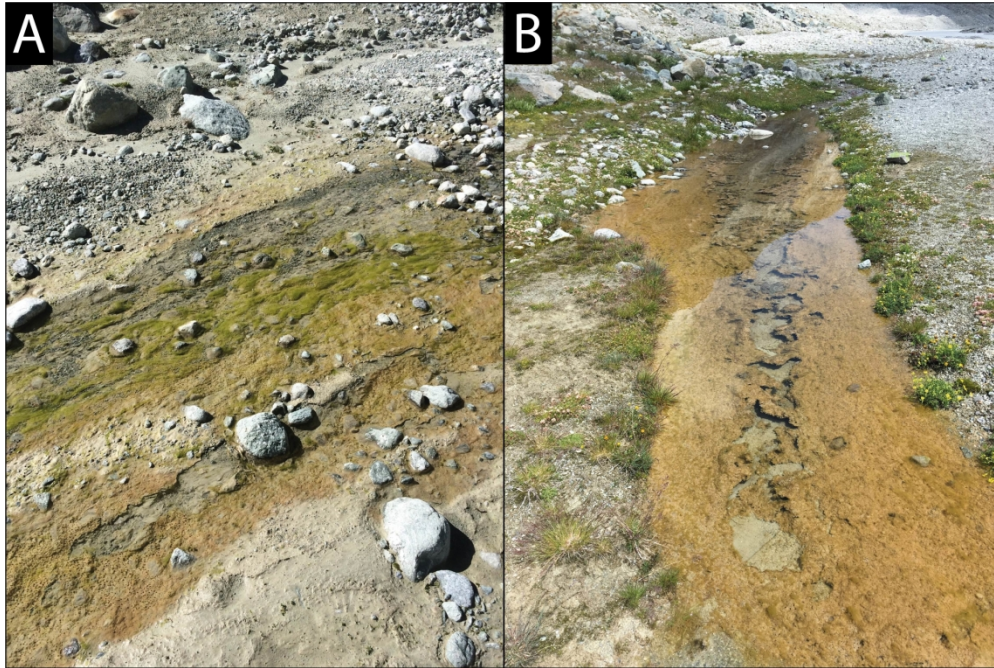
385x581mm (300 x 300 DPI)
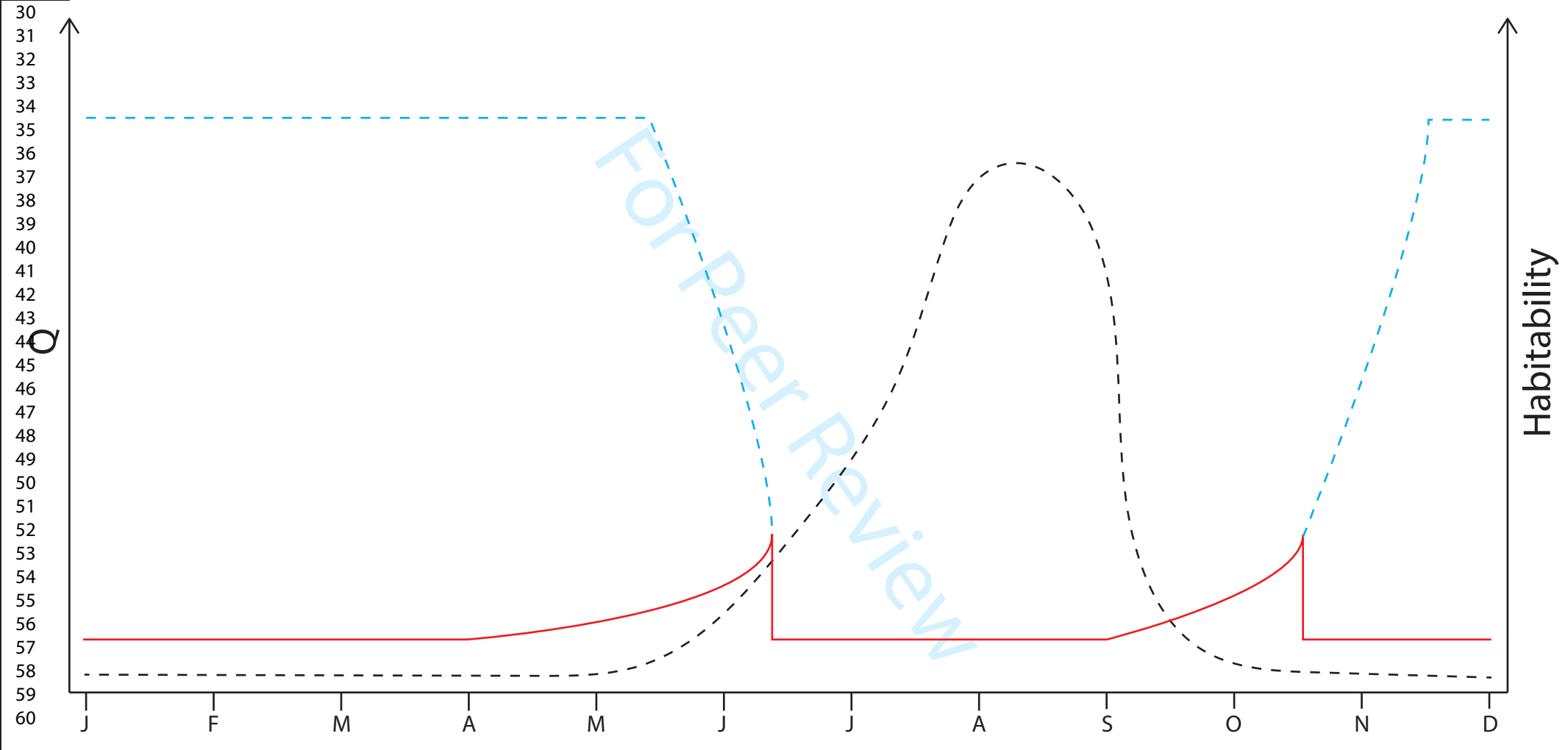
A) Biofilm formation in a stream on a terrace in the Val d'Otemma, Valais, Switzerland; B) A biofilm mat that has formed in a stream in the Val d'Otemma supplied with hillslope-sourced groundwater showing successional colonization of the channel margin by vegetation. The stream is on a terrace about 1 m above the morphodynamically active channel. Note to the right there are stable bar surfaces, also on the terrace, but largely void of primary production due to severe moisture limitations related to well-drained glaciogenic sediments.

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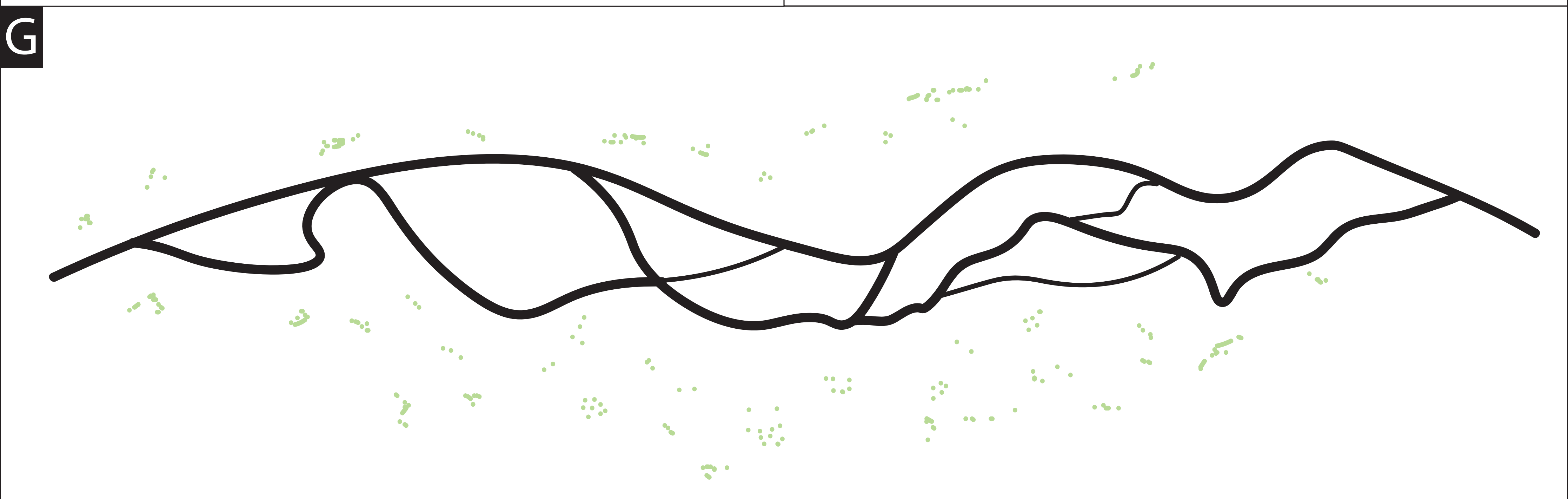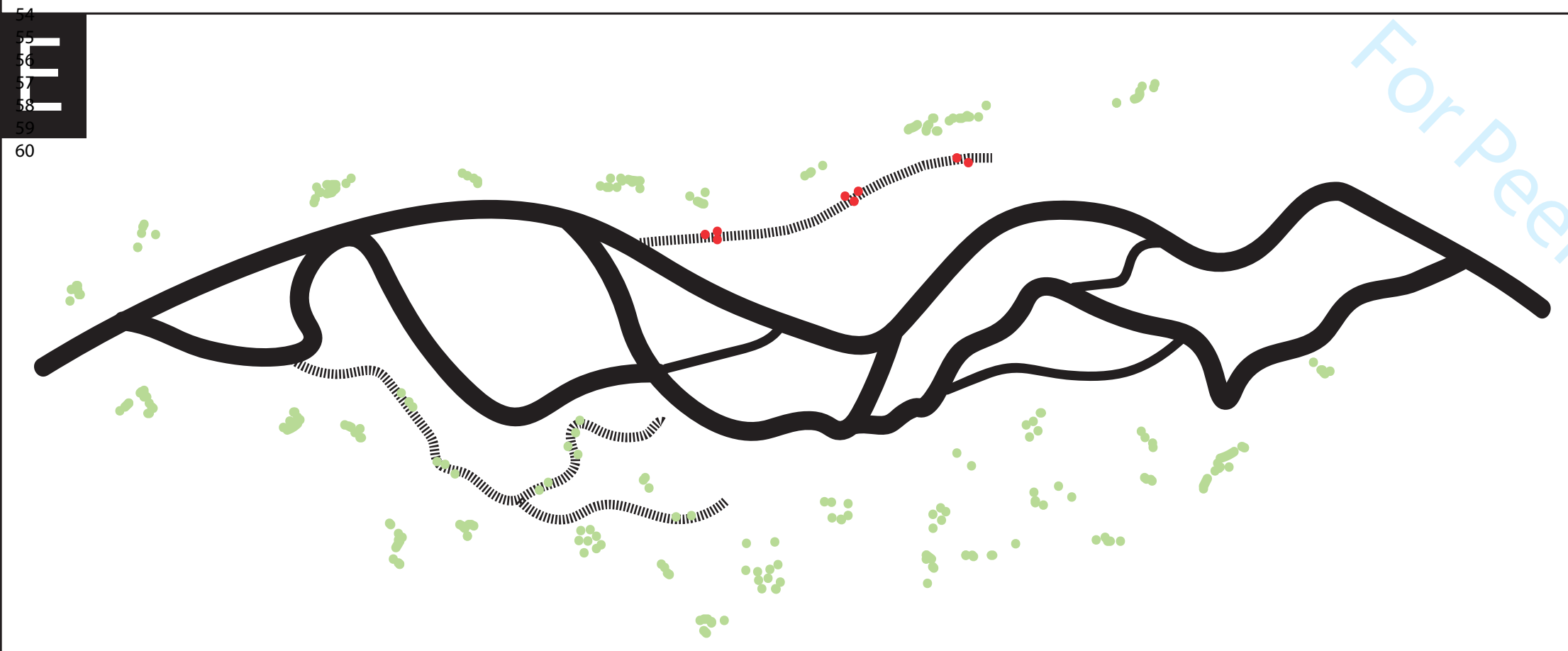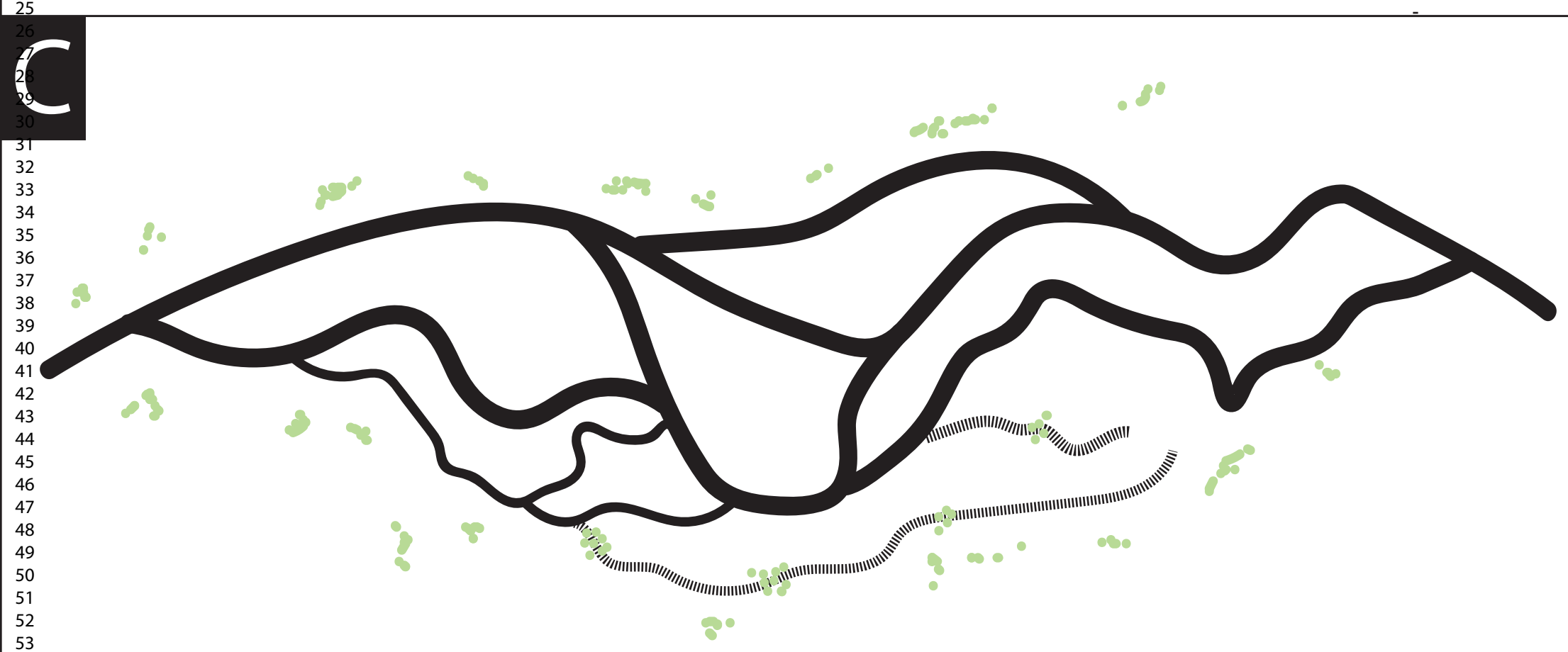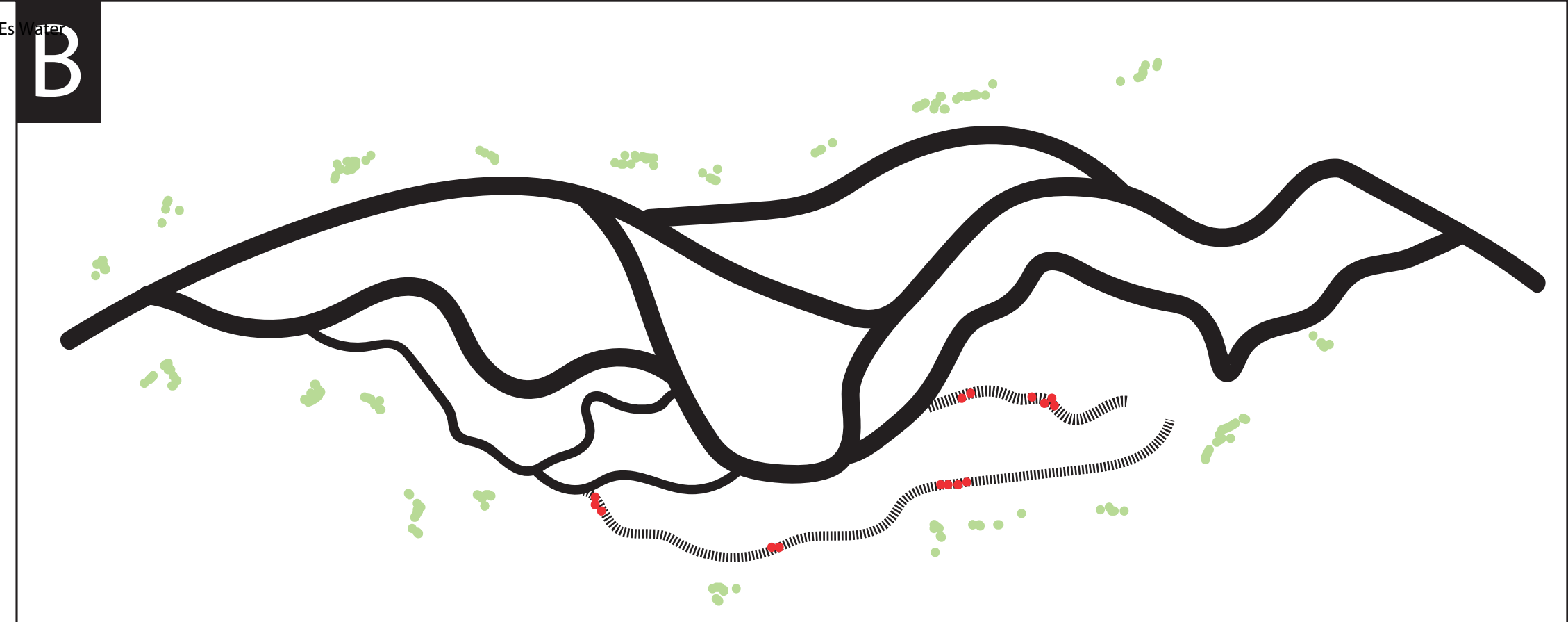
▬▬ Channels on the active plain	░░░ Abandoned channels	• • Vegetation
		• • Biofilm colonies