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A conceptual framework for understanding the biogeochemistry of dry riverbeds through the lens of soil science

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Abstract

Intermittent rivers and ephemeral streams (IRES) encompass fluvial ecosystems that eventually stop flowing and run dry at some point in space and time. During the dry phase, channels of IRES consist mainly of dry riverbeds (DRBs), prevalent yet widely unexplored ecotones between dry and wet phases that can strongly influence the biogeochemistry of fluvial networks. DRBs are often overlooked because they do not strictly belong to either domain of soil or freshwater science. Due to this dual character of DRBs, we suggest that concepts and knowledge from soil science can be used to expand the understanding of IRES biogeochemistry. Based on this idea, we propose that DRBs can be conceptually understood as early stage soils exhibiting many similarities with soils through two main forces: i) time since last sediment transport event, and ii) the development status of stabilizing structures (e.g. soil crusts and/or vascular plants). Our analysis suggests that while DRBs and soils may differ in master physical attributes (e.g. soil horizons vs fluvial sedimentary facies), they become rapidly comparable in terms of microbial communities and biogeochemical processes. We further propose that drivers of DRB biogeochemistry are similar to those of soils and, hence, concepts and methods used in soil science are transferable to DRB research. Finally, our paper presents future research directions to advance the knowledge of DRBs and to understand their role in the biogeochemistry of intermittent fluvial networks.

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Key words (4-6): cross-ecosystem research, drought, sediments, aquatic-terrestrial interfaces, temporary, non-perennial

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1. Introduction

Intermittent rivers and ephemeral streams (IRES) encompass fluvial ecosystems that eventually stop flowing and run dry for some extent of time at some point along their course (Acuña et al., 2014; Larned et al., 2010). While intermittent rivers support water flow most year round but fall dry seasonally (normally in summer), ephemeral streams present dry phases lasting beyond a seasonal period and they transport surface water only after intensive rainfall (Uys and O'Keeffe, 1997; Williams, 2006). IRES are likely to account for at least half of the global fluvial network (Datry et al., 2014; Stanley et al., 1997) and they have been described as being more representative of the world's river systems than those with permanent flow (Datry et al., 2017; Williams, 1988). Recent estimates indicate that IRES represent 69% of total stream length, being the dominant watercourse type in arid and semiarid regions (Schneider et al., 2017). Importantly, flow intermittency is expanding worldwide in response to global warming and increased water extraction for human use (Schewe et al., 2014). As a result, interest in IRES research and management is rapidly growing, but the contribution of IRES to global biogeochemical cycles remains unclear (Datry et al., 2017; Leigh et al., 2016). Most biogeochemical studies of IRES have focused on the transition phases, from wet to dry and from dry to wet (e.g. Arce et al., 2014; Corti and Datry, 2012; Romaní et al., 2006; Skoulikidis et al., 2017a; von Schiller et al., 2015). However the dry phase (i.e. the period when no surface water is present) has received little attention so far (Datry et al., 2017; Steward et al., 2012), which makes the understanding of IRES biogeochemistry still incomplete.

Riverbed sediments of IRES during the dry phase, namely dry riverbeds (DRBs), have been recently recognized as valuable ecotones linking dry and wet phases and hosting aquatic, terrestrial, and amphibious communities (Steward et al., 2012). Still, DRBs are often viewed as biogeochemically inert compared to perennial reaches and intermittent reaches during surface-flow periods (Larned et al., 2010; Steward et al., 2012). In fact, recent studies pose DRBs as relevant sites for organic matter (OM) and nutrient cycling along the fluvial network. For instance, OM processing by microbial communities that remain active during dry conditions likely causes release of considerable amounts of carbon dioxide (CO_2) from DRBs to the atmosphere (Marxsen et al., 2010; Zoppini et al., 2014;

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Zoppini and Marxsen, 2011), even at higher emission rates than flowing streams and being comparable to upland soils (Gómez-Gener et al., 2016; von Schiller et al., 2014). In addition, DRBs play a fundamental role in landscape nitrogen (N) cycling since they are significant sites for ammonia (NH_4^+) oxidation, a process that provides nitrate (NO_3^-) within fluvial networks (Arce et al., 2014; Gómez et al., 2012; Merbt et al., 2016). Despite their potential relevance, DRBs typically are not considered in biogeochemical budgets at the fluvial network scale (Raymond et al., 2013). This is probably because DRBs are excluded from the domains of both aquatic and terrestrial science, and thus conceptually placed in a scientific "no man's land" (Steward et al., 2012).

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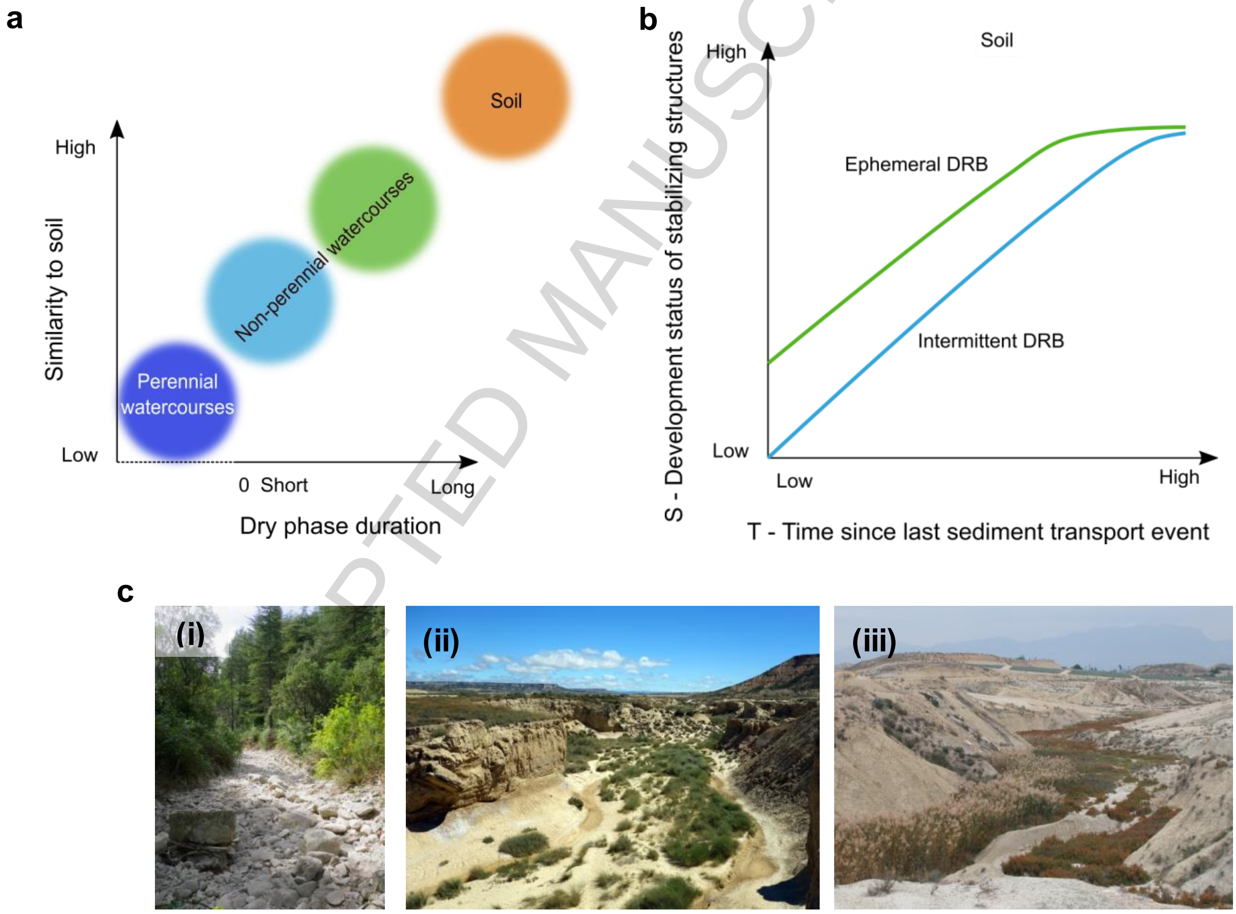

Figure 1. (a) Degree of similarity between soils and different types of watercourses as a function of the duration of the dry phase. (**b**) Conceptual framework indicating how dry riverbeds (DRBs) of non-perennial watercourses (intermittent and ephemeral) may become similar to soils as a function of two main drivers: time since the last sediment transport event (T), and development status of stabilizing structures such as soil biocrusts and/or vascular plants (S). Note that the conceptual framework operates under the spatial concurrence of DBRs and soils involving similar climate, topography,

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parental material and organisms. The conceptual model shows that any flow event reducing T in DRBs will interrupt their trajectory of similarity to soils and move DRBs away from soils; the decrease in similarity resulting from flow resumption events will be more intense in intermittent DRBs (with lower starting point at S) than in ephemeral DRBs (with higher starting point at S). (**c**) DRBs with variable plant coverage: **i**: intermittent stream in France (El Aiguebrun, Vaucluse, photo by B. Launay), **ii**: ephemeral stream in northern Spain (Barranco de las Cortinas, Bardenas Reales, Navarra, photo by D. von Schiller) and **iii**: ephemeral stream in southern Spain (Rambla de la Parra, Murcia, photo by R. Gómez).

Unlike continuously inundated riverbeds of perennial watercourses, DRBs of non-perennial watercourses are transitional habitats that move away from an aquatic to a terrestrial status and become "terrestrialized" by acquiring similar features to nearby soils (**Figure 1a**; Elosegi et al., 2010; Morandi et al., 2014; Thorp et al., 2006; Ward, 1998; Ward et al., 1998). When the constraints imposed by flowing surface water disappear, other constraints similar to those affecting soils will determine the biogeochemistry of DRBs (O'Neill et al., 1986). Similar to that of hydrologically dynamic floodplain systems (Schiemer, 1999), in non-perennial watercourses, the degree of "terrestrialization" and similarity to soils is linked highly to the duration of the dry phase (lack of surface water) and to inundation frequency (e.g. Harms and Grimm, 2012; Harms et al., 2009; Mori et al., 2017). These features are controlled by climate and local geomorphologic conditions, and shape the exposition of DRBs to inundation events (e.g. position in the fluvial network and connection with the main watercourse). Thus, the degree of similarity between soils and DRBs will be more prominent in sites with long dry phases and less frequent flow events (**Figure 1a**). DRBs and soils are composed of a complex mixture of the same constituents (i.e. rocks, minerals, OM, and assemblages of plants, animals and microorganisms). Both habitats are organized in a mosaic-like pattern of bed substrates and pedotops, respectively, and filter, store, and transform energy and nutrients.

Given the potential similarities between DRBs and soils, we suggest that soil science can provide freshwater scientists fruitful information to better understand the biogeochemistry of DRBs and their role in fluvial networks. Research methods, paradigms and models used to investigate biogeochemical processes in DRBs and their response to environmental factors could emerge from soil science rather than from freshwater science. Indeed, biogeochemical concepts in freshwater science that are mostly

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based on perennial running waters cannot be applied strictly to DRBs, e.g. the Nutrient Spiraling Concept (Newbold et al., 1981; Webster and Patten, 1979; but see the Telescoping Ecosystem Model Fisher et al., 1998). Also, because DRBs are shaped by sediment transport and flow events, certain basic principles linked to soil science such as vertical distribution of soil profiles and steady state assumptions based on stability of energy and material budgets over time are difficult to apply to DRBs (Blume et al., 2016; Huggett, 1998; Nadelhoffer et al., 1998). Conversely, DRBs fit into many concepts derived from soil science, especially those regarding biogeochemical responses to water pulses (Austin et al., 2004; Belnap et al., 2005). For example, rainfall and flood events in DRBs lead to increased carbon mineralization and emissions of CO_2 (Fromin et al., 2010; Gallo et al., 2014), a process that has been previously well described in soils and known as the "Birch effect" (Birch, 1958). However, freshwater research has paid little attention to these ideas so far. Given that soil-forming processes (weathering, leaching, mineral formation and destruction, podsolization, and humus development) occur at time scales from years to thousands of years, DRBs can be considered as a type of relatively early stage soil type, like fluvisols. These are young soils that develop from alluvial deposits with weak horizon development that are flooded periodically by surface waters or rising groundwater (Blume et al., 2016; FAO, 2006; Grimm et al., 2003; Soil Survey Staff, 2014).

We propose that DRBs can be conceptually understood as young soils that evolve gradually towards a more mature stage soil-like, a process functioning from two main forces (**Figure 1b**): time since last sediment transport event (T), and development status of stabilizing structures such as soil crusts or vascular plants (S). We consider as reference an upland soil, since riparian soils or floodplains can be seen as intermediate stages in this evolution of similarity. The proposed conceptual framework is based on the assumption that soils and DRBs occur in close proximity so that parent material, climate, topography and biotic community can be considered equivalent (i.e. concurrent; see section 2 for further details). For example, a valley soil where there is much deposition of fine material and soil depth is high (Blume et al., 2016) should not be compared with a headwater DRB where erosion is high and the riverbed is dominated by coarse material, which is more similar to a hillslope soil (Allan and Castillo, 2007; Blume et al., 2016). The particular hydrological regime of a non-perennial

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watercourse has fundamental implications for our conceptual model by determining the degree of development of stabilizing structures (S) at the beginning of T (**Figure 1b, and c ii, iii**). In ephemeral streams, DRBs often present a certain degree of terrestrialization with the presence of terrestrial plants as stabilizing structures (Fossati et al., 1999; Stromberg et al., 2017) similar to those developed in gravel bars subject to episodic dry and flood phases (**Figure 1b, and c ii, iii**; e.g. Bätz et al., 2014; Mardhiah et al., 2014; McBride and Strahan, 1984). Thus, in our conceptual framework, DRBs of ephemeral streams may exhibit features more similar to soils by showing a higher degree of development of stabilizing structures (higher S, **Figure 1b, Figure 1c ii, iii**) when compared to DRBs of intermittent rivers that commonly lack such types of vegetation (**Figure 1b, Figure 1c i**). Further, any flow resumption determining the duration of T will temporarily move back the DRB to the aquatic state, thereby resetting their "trajectory" toward soil; this reset being more intense in intermittent than ephemeral DRBs (**Figure 1b**).

Conceptually, from this perspective, DRBs increasingly resemble soils along structural and functional dimensions as the hydrological regime shifts from intermittent (time "T" seasonal- dependent) to ephemeral (time "T" supra-seasonal dependent with episodic flow events; Uys and O'Keeffe, 1997; Williams, 2006). Based on this conceptual framework, we explore the potential of using knowledge from soils to study the biogeochemistry of DRBs by comparing key structural (physical and microbiological) and functional (biogeochemical processes) attributes of both types of habitats. As exposed above, our comparisons are based on the assumption of spatial concurrence of both habitats. Because the research interest of the authors centers on OM and nutrient cycling, the treatment of biogeochemistry refers mainly to these functional properties. By comparing soils and DRBs, we aim to improve the understanding of IRES biogeochemistry and provide insights for modeling at multiple spatio-temporal scales.

2. Physical structure of DRBs and soils and their geomorphological drivers

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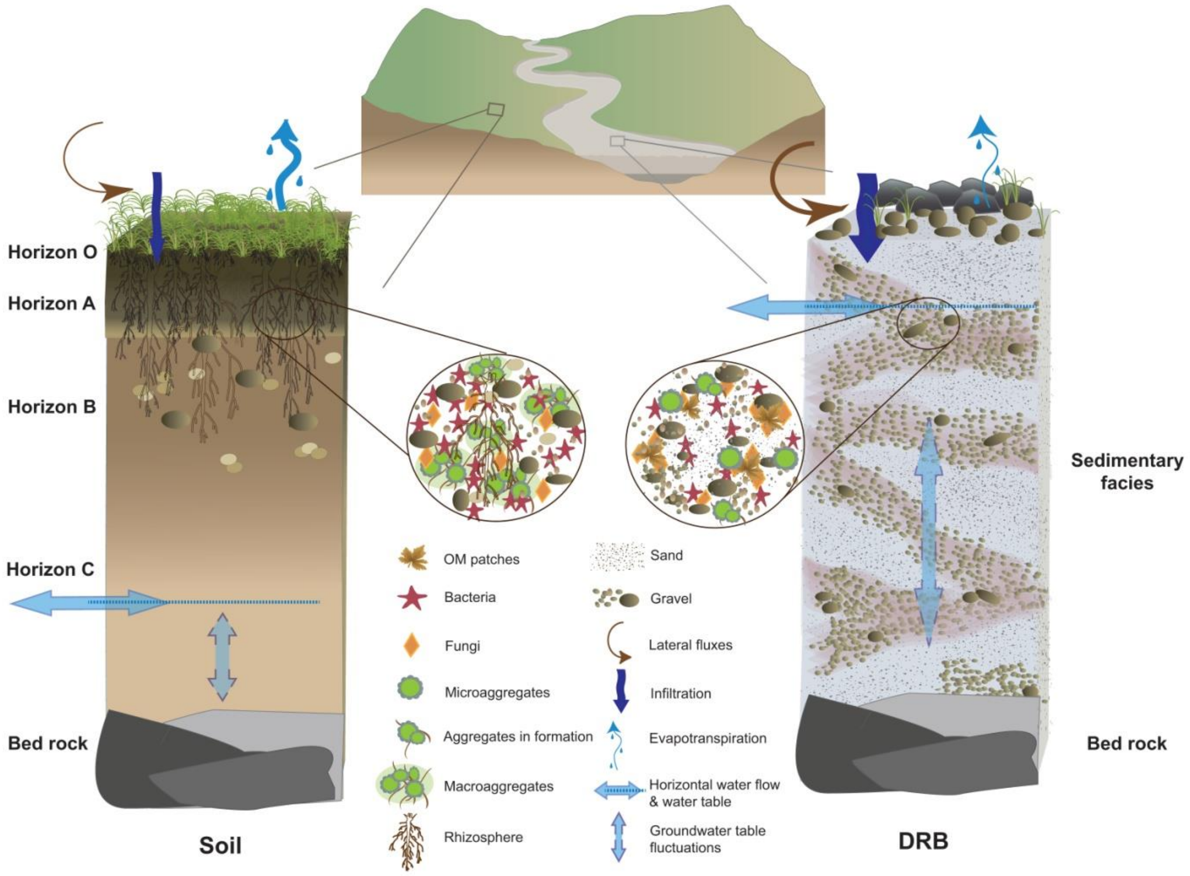

Figure 2. Diagram of a soil profile (left) and a dry riverbed profile (DRB, right) showing major similarities and differences in physical, geomorphological, hydrological and biological properties. Soil formation is mainly a local process that results in the development of its horizons that further determine their physical, microbial and biogeochemical features. DRB structure and formation depend on deposition and sorting processes during sediment transport that result in sedimentary facies characterized by sorting of sediment particles. During the dry phase, local formation processes will favour the development of aggregates in DRBs. The position of DRBs and soils within the landscape will influence oscillations in groundwater level, likely more frequent in DRBs that have subsurface flow and lateral fluxes. The presence of vegetation in soils will favour evapotranspiration and limit the infiltration of water, while the low biomass or complete lack of vegetation of DRBs will reduce evapotranspiration and favour infiltration of water as well as temperature fluctuations and gas exchange. The presence of roots and rhizosphere in soils will further favour the development of aggregates. OM will be more patchily distributed in DRBs as a result of downstream transport and deposition. Microbial communities will differ between soils and DRBs as a result of the different content and distribution of OM and presence of vegetation.

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Soil formation occurs through disintegration, decomposition, recomposition and aggregation of mineral material contained in exposed rocks by physical and chemical processes. This material is further conditioned by biological activity and culminates in the formation of the characteristic soil profile (**Figure 2**; Blume et al., 2016; Hillel, 2003). A soil profile is composed of a number of horizontal layers (i.e. soil horizons) that differ in colour, physical structure and chemical characteristics from the parent material (**Figure 2**; Blume et al., 2016; Jones et al., 2005; Weil and Brady, 2016). In contrast, DRBs result from the transport and deposition of sediments as water makes its way downstream (Gordon et al., 2004). Transport and deposition result in a complex arrangement in strata, characterized by overlapping sedimentary layers of different grain size distributions (**Figure 2**; Bridge, 2003; Gordon et al., 2004). Due to different formation processes, parent material may differ with soils being mainly composed of a mixture of organic and mineral compounds of autochthonous origin while DRBs can be considered being composed of allochthonous material. Still, DRBs are inherently linked to the eroded soils and slopes from which they come from (Boix-Fayos et al., 2006; Boix-Fayos et al., 2015; Jaeger et al., 2017; Rhoton et al., 2006). Due to this strong link between soils and DRBs, concurrence must be considered when applying our conceptual model (see above).

The genesis of both soils and DRBs is linked to the topography, lithology and geomorphological dynamics occurring at different spatial and temporal scales. At the catchment scale, and depending on local soil characteristics, land-use, climate, erosion processes (rill, inter-rill, gully, bank and channel erosion, landslides) and their interaction will ultimately determine the particle size, the amount and quality of OM and nutrients transported and redistributed within the catchment, and to the fluvial network (de Vente and Poesen, 2005; Haregeweyn et al., 2008; Hoffmann et al., 2013; Kusnierz and Sivers, 2018; Nadeu, 2013; Nadeu et al., 2012; Nadeu et al., 2011; Scott et al., 2013; Wang et al., 2010). At hillslope and reach scale, geomorphology will determine the physical characteristics of soils and DRBs. For instance, in a sub-humid Mediterranean catchment, the similarity between soils and alluvial bars and wedges in some physico-chemical properties (e.g. texture, micro-aggregates, and organic carbon content) strongly depended on the distance from source areas and sediment connectivity (Boix-Fayos et al., 2015; Nadeu et al., 2012; Nadeu et al., 2011).

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The formation processes result in differences in the physical characteristics of soils and DRBs (**Table 1**). From a biogeochemical perspective, water content, bulk density, OM, hydraulic conductivity and fine particle content are the most relevant physical properties. These properties modulate gas and water fluxes, temperature distribution and habitat availability (Blume et al., 2016). In soils, gas fluxes and infiltration and evaporation of water can be reduced by the organic horizon with abundant fine particles (**Table 1** and **Figure 2**; Franzluebbers, 2002; Minasny and McBratney, 2017). Fine particles reduce porosity, enhance thermal conductivity and buffer temperature oscillations (Blume et al., 2016). As a result of the transport and deposition formation processes, DRBs tend to have coarser particles (more sand and less clay) compared to soils, and they are generally depleted in OM and nutrients that are patchily distributed (Boix-Fayos et al., 2015; Frossard et al., 2015; Gómez-Gener et al., 2016; Smith et al., 2013; Stacy et al., 2015). As observed in bare soils (e.g. Smits et al., 2012), the coarser texture and lower OM in DRBs will result in higher water infiltration and evaporation, gas fluxes, and oscillations in temperature (**Table 1**; Blume et al., 2016; Zribi et al., 2015).

Physicochemical property	Soils	DRBs	Reference
Spatial arrangement	Horizons (*in situ* formation)	Sedimentary structures (deposited material)	FAO, 2006
Profile depth	variable	variable	
Dominant grain size	< 2mm	> 15mm	Boix-Fayos et al., 2015; Frossard et al., 2015; Gómez-Gener et al., 2016; Stacy et al., 2015
Sand content (2000-63 µm)	low	high	Boix-Fayos et al., 2015; Doetterl et al., 2012; Gómez-Gener et al., 2016; Nadeu et al., 2011; Rhoton et al., 2006
Clay content	high	low to medium	Boix-Fayos et al., 2015; Doetterl et al., 2012; Gómez-Gener et al., 2016; Rhoton et al., 2006
Macroaggregates (>2mm)	high	low	Bätz et al., 2014; Mardhiah et al., 2014
Microaggregate (63-250 µm)	high	low	Bätz et al., 2014; Mardhiah et al., 2014

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Bulk density (g cm^{-3})	low	high	Nadeu et al., 2011
Water holding capacity (%)	high	low	Gómez-Gener et al., 2016
Porosity*	low	high	
Compaction*	high	low	
Hydraulic conductivity*	low	high	
Cation Exchange Capacity (CEC)	high	low	Frossard et al., 2015
OM origin	autochthonous	mostly allochthonous	Datry et al., 2018
OM content	high, decreases with soil profile depth	low, regardless of sediment profile depth	Boix-Fayos et al., 2015; Nadeu et al., 2012; Nadeu et al., 2011; Rhoton et al., 2006; Stacy et al., 2015; Wang et al., 2010
N content	high	low	Boix-Fayos et al., 2015; Gómez-Gener et al., 2016; Wang et al., 2010
C:N	high	low	Boix-Fayos et al., 2015

* Based on grain size distribution and clay content

Table 1. Comparison of key physico-chemical properties of soils and dry riverbeds (DRBs).

During the dry phase, the physical characteristics of DRBs will be more influenced by local formation processes as in soils. A key property of soils will begin to develop and gain significance: so-called aggregates (**Figure 1b and 2**; Mardhiah et al., 2014; Totsche et al., 2017). Aggregates (micro- and macro-) consist of a group of soil particles that adhere to one another more strongly than to surrounding soil particles (**Table 1**, **Figure 2**; Follet et al., 2009). Aggregates result from the interaction of many factors, including micro-environmental conditions (mainly water availability and temperature), soil properties, and presence of bioengineers (plants, mycorrhizal hyphae, invertebrates and microorganisms; An et al., 2010; Bätz et al., 2014; Chotte, 2005; Kay, 1998; Miltner et al., 2012; Verchot et al., 2011). Depending on their size and porosity, aggregates influence the physical properties of soils: movement and storage of water, diffusion of solutes, redox gradients, microbial community structure and vegetation development (Gregorich et al., 2003; Mora-Gómez et al., 2015;

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Sollins et al., 1996; Verchot et al., 2011). Aggregates are often considered as biogeochemical hotspots (Ebrahimi and Or, 2016; Lee et al., 2012; Rillig et al., 2017; Vos et al., 2013); in fact, soil quality is often expressed as the degree of aggregation (Bronick and Lal, 2005). Raindrops, erosion, scouring and drying easily disrupt aggregates (Blankinship et al., 2016; Boix-Fayos et al., 2015; Hillel, 2003), and once they reach the stream by water flow runoff, they undergo flocculation processes that totally alter their physical structure (Droppo et al., 2005). Therefore, the presence and significance of aggregates in DRBs at early stages of the dry period might be limited compared to soils and are increasingly formed as roots and fungi develop (**Figure 2**; Bätz et al., 2014; Mardhiah et al., 2014).

Vegetation establishment plays a key role in the physical characteristics of DRBs. First, the development of vegetation and biocrusts stabilizes the sediment (**Figure 1b**) and is a pedogenic force that modifies its physical structure that favors the development of aggregates and macropores, creating new habitats (rhizosphere) for terrestrial microorganisms (Bätz et al., 2014; Gutiérrez and Jones, 2006; Verboom and Pate, 2006). Second, similar to the effect of riparian vegetation, the presence of vegetation in DRBs can modulate exposure to wind and solar radiation as well air humidity, ultimately determining temperature distributions and water and gas fluxes (**Figure 1 c iii**; Fossati et al., 1999; Hillel, 2003; Li et al., 2016; Stromberg et al., 2017). The development of vegetation in DRBs is also associated to geomorphological processes, such as river incision, that cause changes in the frequency and intensity of sediment transport events and lowers groundwater levels (Auble et al., 1994; Bombino et al., 2013; Ellery et al., 1993; Poff, 1997). Due to their position in the landscape (i.e. topography), the groundwater table in DRBs tends to be closer to the surface than in soils; in fact, DRBs can support subsurface flow despite the lack of continuous flowing surface water (**Figure 2**; Costigan et al., 2016, 2017; Marxsen et al., 2010). As a result of the more superficial groundwater table and/or subsurface flow, riparian ecosystems that border perennial to intermittent rivers and streams in dryland regions have substantially more biomass and greater productivity than the surrounding terrestrial vegetation (Scott et al., 2013). Therefore, the development of vegetation and stabilizing structures in DRBs might be favoured by groundwater table and subsurface flow as in ephemeral streams (**Figure 1c iii**).

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3. Biogeochemistry of DRBs and soils

In this section, we compare the main microbial and biogeochemical properties involved in OM and nutrient cycling in soils and DRBs by using information from the available literature and by examining how different physical factors (e.g. vegetation, texture; **Figure 2** and **Table 1**) can drive differences in specific biogeochemical properties (**Table 2**). In general, we approach the comparison between the two habitat types from the temporal perspective of desiccation of DRBs (early or late stages). Due to the relevance of water availability for biogeochemical reactions in water-limited systems such as DRBs, we further examine and compare the functional response of soils and DRBs to changes in water availability.

Biogeochemical process	Soils	DRBs	References
Leaf litter decomposition (d^{-1})	0.0012-0.0072[d,e,f]	0.0005 - 0.0032[a,b,c]	[a]Abril et al., 2016; [b]Corti et al., 2011; [c]Riedl et al., 2013; [d]Almagro et al., 2010;[e]Langhans et al., 2006; [f]Langhans et al., 2008
Net primary production ($mg\ C\ m^{-2}\ d^{-1}$)	800-3000[g,,h, d]	No data available	[g]Ni et al., 2001; [h]Michaletz et al., 2014
CO_2 emissions measured *in situ* (chamber; $mg\ C\ m^{-2}\ d^{-1}$)	65– 2500[i, j]	74– 1728[i-j, d, k, l, m]	[i]Gómez-Gener et al., 2016; [j]Gómez-Gener et al., 2015;[k]Bond-Lamberty and Thomson, 2010; [l]Raich and Schlesinger, 1992; [m]Raich et al., 2002
Extracellular enzyme activities ($nmol\ h^{-1}\ cm^{-2}$)			
β-glucosidase	3320[n]	5 – 225[o]	[n]Sinsabaugh et al., 2008; [o]Timoner et al., 2012
Leucine aminopeptidase	1450[n]	0 – 180[o]	
Alkaline phosphatase	5300[n]	50 – 300[o]	

*Net primary production was computed as the sum of annual production of roots, stems, branches, and reproductive (when available) and foliage components.

Table 2. Comparison of biogeochemical processes in soils and dry riverbeds (DRBs). When paired studies were not available, individual studies undertaken under arid, semiarid, and Mediterranean

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conditions were selected by assuming that arid and semiarid DRBs would likely be the most similar to uphill soils.

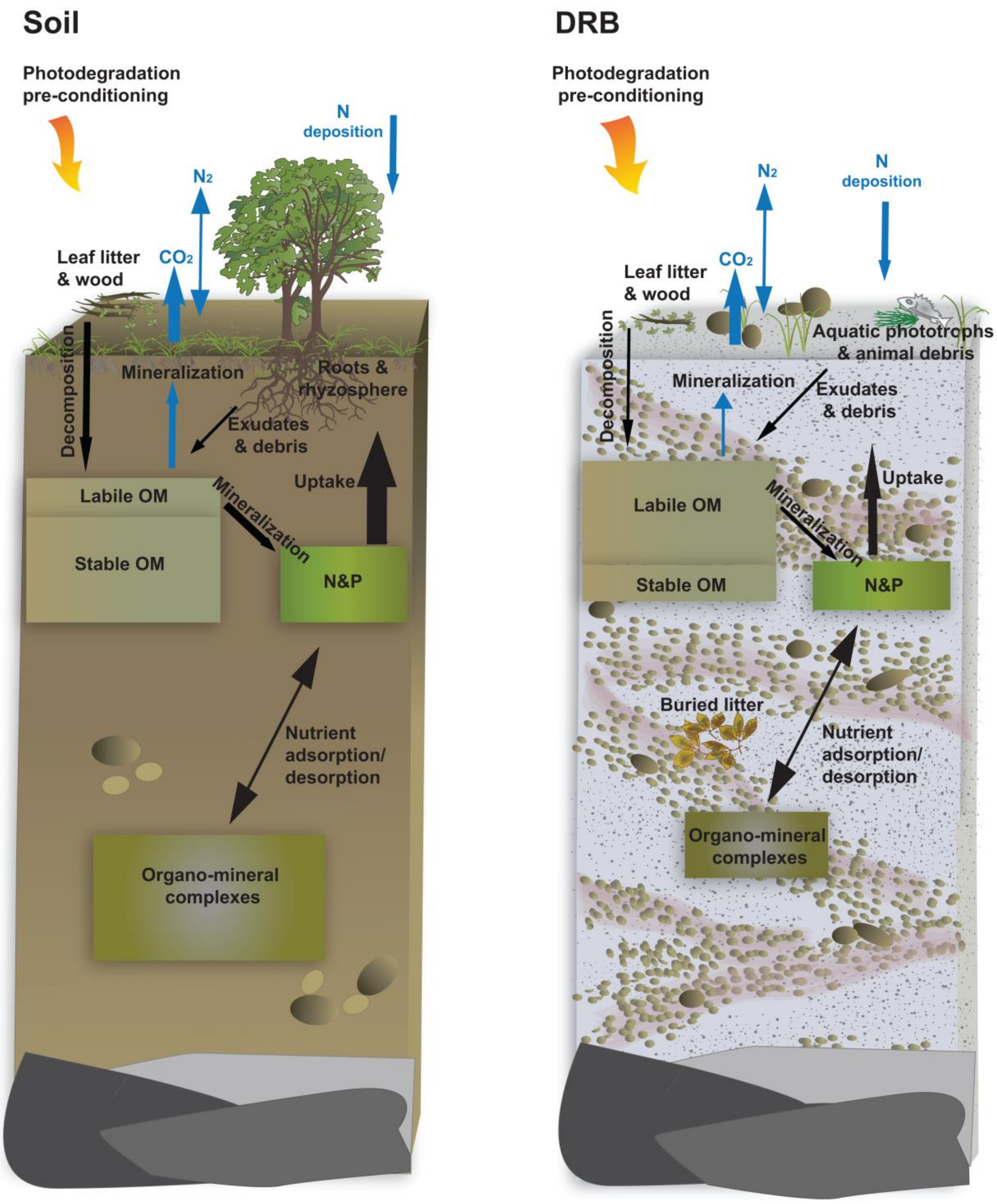

Figure 3. Diagram representing the main processes and fluxes of organic matter (OM) and nutrients (N and P) occurring in soils and dry riverbeds (DRBs). Different sizes of boxes and arrows represent

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differences in the relative importance of each compartment and process, respectively. Gas fluxes are represented in blue color. Terrestrial OM sources dominate in soils, while both aquatic and terrestrial OM sources are present in DRBs. The OM pool is divided into labile and stable OM, the latter being more relevant in soils together with organo-mineral complexes (i.e. associations of organic matter and mineral particles) that play an important role in adsorption-desorption processes of primary nutrients (N and P). The rhizosphere in soils plays a relevant role in nutrient dynamics as well as being a source for labile dissolved OM (DOM). In DRBs, sediment mobility can determine the amount of litter material buried in deep sediments, acting as OM decomposition hotspots as well as microbial refuge.

3.1 Microbial community composition

Microbial communities regulate biogeochemical cycles in ecosystems (Rousk and Bengtson, 2014). The degree of similarity between DRBs and soils in terms of microbial community composition depends both on deterministic (i.e. environmental filtering) and stochastic processes (i.e. dispersal from adjacent terrestrial ecosystems). Similar to soils, microbial community composition in DRBs is likely driven by OM and nutrient availability, colonizable surfaces, redox conditions, texture, aggregates and humidity (Girvan et al., 2003; Johnson et al., 2003; Marschner et al., 2003; Rillig et al., 2017). In DRBs, together with increases in OM and nutrients, the progressive development of aggregates can contribute to enhance the degree of similarity of microbial communities with soils. While recent research suggests that bacterial, fungal and archaeal communities along a terrestrial-aquatic gradient are dominated by specialist microorganisms specific to a particular habitat (Monard et al., 2016), a study in boreal systems concluded that between 20-35% of freshwater bacteria are of terrestrial origin (Ruiz-González et al., 2015). Therefore, despite local differences, microorganisms of terrestrial origin could increase the degree of similarity between soils and DRBs in combination with increases in OM content and aggregate development. Together with physical properties of sediment/soil, the degree of similarity between DRBs and soil microbial communities also will be driven by dispersal and colonization from adjacent terrestrial ecosystems, groundwater, and hyporheic zones of taxa with specific habitat requirements (Febria et al., 2012; Febria et al., 2015; Mering et al., 2007; Monard et al., 2016; Sabater et al., 2016; Timoner et al., 2014).

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In addition to dispersal and the physical properties of soils and DRBs, we expect the similarity between DRB and soil communities to be linked to water fluctuations (drying, subsurface and surface flow, groundwater table oscillations and rainfall). Drying stress in soils is a fundamental driver of compositional changes of communities that selects taxa able to cope with osmotic stress (Fierer and Schimel, 2002; Schimel et al., 2007; Zoppini et al., 2014; Zoppini and Marxsen, 2011; Pohlon et al., 2013). Water fluctuations can cause drying-rewetting stress, thereby selecting osmotic stress resistant microbial communities in both soils and DRBs (Borken and Matzner, 2009; Fromin et al., 2010; Lundquist et al., 1999; Schimel et al., 2007). Recent research has reported similar mechanisms between soils and DRBs to cope with drying-rewetting stress; for instance, thicker cell walls in gram positive bacteria and fungi (Lennon et al., 2012; Manzoni et al., 2006; Schimel et al., 2007; Zeglin et al., 2013), and production of extracellular polymeric substances by biofilms to increase sediment/soil water holding capacity and growth at lower water potentials (Chenu, 1993; Flemming and Wingender, 2010; Or et al., 2007; Romaní et al., 2013; Rosenzweig et al., 2012; Sabater et al., 2017).

3.2 OM cycling

In general, the higher plant biomass developed in soils compared to DRBs determines higher OM standing stocks and higher C:N elemental ratios in soils than in DRBs (**Table 1**). Moreover, while soils are fueled only by terrestrial OM sources, both aquatic and terrestrial sources contribute to OM pools in DRBs (**Figure 3**). At the first stages of drying in DRBs, OM stocks from the preceding aquatic phase (e.g. biofilms and macrophytes) are especially relevant (Ylla et al., 2010). These autochthonous sources are of high nutrient quality (low C:N elemental ratio; Artigas et al., 2008) and provide labile OM that can support high microbial activity, similar to patterns described in primary soils after glacier retreat or in deserts (Bradley et al., 2015). Furthermore, variability in OM stocks in DRBs during early desiccation stages can result in higher heterogeneity of DOM and particulate OM (POM) compared to soils.

Throughout the dry period in DRBs, we expect that both OM quantity and quality of DRBs become similar to those of surrounding soils due to leaf litter inputs from riparian zones and development of

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terrestrial vegetation (Acuña et al., 2007; McClain et al., 2003; Stegen et al., 2016b). In soils, root production represents a considerable OM source (Schmidt et al., 2011; Silver and Miya, 2001; Williams, 1988). While roots are a more stable or recalcitrant OM source than leaf litter (Austin et al., 2009; Kemp et al., 2003), root exudates provide a labile C source to microbial assemblages of rhizospheres (Wagener et al., 1998) that is lower in DRBs (Kallenbach et al., 2016). In general, higher and more stable OM content is expected in soils (Schimel and Schaeffer, 2012) and lower but more labile OM content is expected in DRBs (**Figure 3**; Axmanová and Rulík, 2005; Trulleyová et al., 2003). However, this general pattern may be modified in arid and semiarid regions where vegetation is limited to riparian zones and within DRBs. Here, a greater amount of OM may accumulate in DRBs compared with adjacent soils (**Figure 1c iii**; Fossati et al., 1999; Steward et al., 2012).

Disparities in OM quality and quantity between soils and DRBs may translate as differences in OM decomposition rates and ultimately in C cyling (Belay-Tedla et al., 2009; Swift et al., 1979). However, other enviromental and biological factors also should be taken into account (pH and microbial stoichiometry demand; Schimel and Schaeffer, 2012; Sinsabaugh, 2010; Sinsabaugh and Follstad Shah, 2011) as well as the interaction between stable OM and labile OM pulses (i.e. priming; Kuzyakov, 2010). In soils and DRBs, extracellular enzyme activities (EEAs) exert a strong control on microbial decomposition of OM (Burns et al., 2013), even under dry conditions (Zoppini et al., 2014; Zoppini and Marxsen, 2011). The presence of specific EEAs also reflect the origin and quality of OM (Chróst, 1991; Kotroczó et al., 2014). For instance, the ratio of β-glucosidase (involved in the decomposition of simple polysaccharides) to phenoloxidase activity (involved in the degradation of lignin compounds) is reduced in soils in contrast to streambed sediments, suggesting sediment OM is more labile than soil OM (Sinsabaugh et al., 2012). The greater capacity to degrade stable OM compounds in soils can be linked to higher fungal biomass in terrestrial ecosystems because fungal communities play a major role in ligno-cellulose degradation (Burns et al., 2013; Romaní et al., 2006).

Disparities in nutrient availability and OM stoichiometry can also determine contrasts in OM bioavailability and decomposition between soils and DRBs. For instance, decomposing OM generally

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exhibits higher C:N elemental ratios in soils than DRBs (**Table 1**), and thus greater N limitation is expected in the former. Lower C:N elemental ratios together with lower OM content suggest heterotrophic activity to be constrained by C availability to some extent in DRBs. We thus hypothesize that this might determine higher values of C to N acquisition enzymes in DRBs compared to soils (**Table 2**; Sinsabaugh et al., 2012).

Differences in OM cycling between DRBs and soils can also be the result of a distinct contribution of terrestrial invertebrates to OM degradation. Terrestrial invertebrates can play a relevant role in the pre-conditioning of POM in DRBs, especially at the beginning of the dry phase when they are attracted by fresh POM of aquatic origin (e.g. dead algae, invertebrates, and fish; Corti and Datry, 2012). Yet, the action of invertebrates in soil OM cycling can persist over time in both shallow and deep layers (Doblas-Miranda et al., 2009).

Abiotic factors are also important drivers of OM decomposition. For instance, in open canopy DRBs or soils decomposition of OM can be strongly influenced by solar radiation and temperature (Almagro et al., 2017; Lee et al., 2012; Steward et al., 2012). Exposition to solar radiation promotes photodegradation and chemical alterations of plant material (Almagro et al., 2015), conditioning it for subsequent biodegradation (del Campo and Gómez, 2016; Fellman et al., 2013). The effect of solar radiation on OM degradation is expected to be higher in DRBs than in soils because vegetation cover tends to be lower in the former (**Figure 3**).

In terms of leaf litter decomposition, information gleaned from the literature indicates that decomposition rates are higher in soils than DRBs (**Table 2**). This pattern can reverse if considering how high organic C decomposition rates can be in the hyporheic zone of some IRES (Burrows et al., 2017). In fact, recent studies addressing direct comparisons of CO_2 emissions in the two habitats showed that DRBs are comparable to upland soils (Gómez-Gener et al., 2016; von Schiller et al., 2014). To obtain a complete view of CO_2 fluxes from DRBs, data on net primary production is still required (**Table 2**). Temperature, moisture, and texture are important drivers of CO_2 emissions in both soils and DRBs (Almagro et al., 2009; Almagro et al., 2013; Gómez-Gener et al., 2016). Yet, OM

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composition could influence CO_2 emissions to a greater extent in soils than in DRBs, where OM availability could play a major role (Artigas et al., 2008; Gómez-Gener et al., 2016). Therefore, under equal temperature and moisture conditions, respiration could be limited by C to a major extent in DRBs compared to soils.

3.3 Nutrient cycling

There are essential differences between soils and DRBs in how assimilatory and dissimilatory processes regulate nutrient cycling (**Figure 3**). One distinctive aspect regards nutrient availability. In soils, most organic N and phosphorus (P) is bound to humic substances, which may be less available to microorganisms than inferred by elemental ratios (Nannipieri and Eldor, 2009). In contrast, labile sources of organic N and P in DRBs such as decaying biofilms provide labile OM and nutrients, at least during early stages of drying. In vegetated soils, roots and fungal hyphae are responsible for most N and P uptake, and they actively transport nutrients from sites of nutrient supply to sites of nutrient demand (e.g. Fellbaum et al., 2014; Ratliff and Fisk, 2016; Robertson and Groffman, 2015; Unger et al., 2016; Wagener et al., 1998). In DRBs, however, nutrient allocation is driven by photoautotrophic and heterotrophic uptake by microbial assemblages. Noteworthy, differences in nutrient uptake between soils and DRBs may become less obvious when plants develop in DRBs as they may outcompete microbes for nutrient uptake (Baldwin and Mitchell, 2000; Cavanaugh et al., 2006).

Atmospheric deposition and N_2 fixation can be important sources of inorganic N in soils and DRBs (**Figure 3**). Since vegetation has been shown to strongly regulate atmospheric N deposition (Aguillaume et al., 2017; Fenn and Poth, 2004), we expect this process to be higher in soils than DRBs because of higher crust levels and vegetation canopy cover in the former (Belnap et al., 2005). Yet, these differences will ultimately depend on climate and atmospheric pollution, and will disappear as the time since last sediment transport event passes (**Figure 1b**).

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As in soils, oxygenation associated with drying creates conditions suitable for aerobic ammonification and nitrification (e.g. Cavanaugh et al., 2006; Gómez et al., 2012; Tzoraki et al., 2007). As a result, inorganic N ($NH_4^+$and NO_3^-) accumulates in DRBs as desiccation progresses with time (Arce et al., 2014; Gómez et al., 2012; Merbt et al., 2016). On the contrary, denitrification, an anaerobic process that contributes to the permanent removal of N from any ecosystem (Seitzinger, 1988), is likely low in soils and DRBs because of low or null water saturation conditions, which impede oxygen diffusion and limit anoxic environments. Occasionally, at early stages of drying (water saturated sediments) or during flood events, DRBs can support extended oxygen-depleted habitats suitable for denitrification with higher rates than in upland soils, similar to that in floodplains (Baker and Vervier, 2004; Valett et al., 2005). However, the availability of an electron acceptor (e.g. NO_3^- or sulfate) and sufficient C to support microbial metabolism also are required for denitrification to occur. Often, highest denitrification rates have been detected where NO_3^- intercepts C rich sites such as plant rooting zones (Jacinthe et al., 1998; Schade et al., 2001). Thus, limited denitrification in well-oxygenated sediments of DRBs at late stages of drying can be alleviated when plants develop in the stream channel, which provide a source of labile C and can promote anoxic microsites within DRBs, and ultimately stimulate heterotrophic metabolism (Schade et al., 2001).

Regarding P cycling, there is little information available for either soils or DRBs. In soils, weathering and mineralization are the most important sources of P (Margalef et al., 2017; Turner et al., 2005), while mineralization in well-aerated porous media may be the predominant P source in DRBs (**Figure 2**). P dynamics are mainly driven by physical and chemical properties of soils and sediments (e.g. Khalid, 1989). P can adsorb to OM, carbonate and clays and also immobilized by biota. Given that DRBs may contain less OM and clay particles than soils, P adsorption is expected to be lower in DRBs. Dieter et al. (2015) and Kinsman-Costello et al. (2016) showed that drying reduced P adsorption and stimulated P mineralization in dry lake sediments, which led to increases in the proportion of labile and soluble P forms. Similarly, mineralization of phosphorylated OM remains active during sediment drying in DRBs (Marxsen et al., 2010; Zoppini et al., 2014; Zoppini and

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Marxsen, 2011). As a result, a significant pulsed release of soluble P can occur upon rewetting in DRBs (Keitel et al., 2016; Kinsman-Costello et al., 2016).

3.4 Water as a fundamental driver of biogeochemical variability in soils and DRBs

A major physical factor influencing the variability of biogeochemical processes in soils and DRBs is water availability (Blume et al., 2016; Sabater et al., 2016). Increases in soil water availability (rain, dew, changes in groundwater table) burst respiration, a phenomenon known as "Birch effect" (Birch, 1958; Kim et al., 2012; Placella et al., 2012). In DRBs, following increases in water availability, similar responses have been reported for respiration (Baldwin and Mitchell, 2000; McIntyre et al., 2009; Riedl et al., 2013), primary production (Timoner et al., 2012), nitrification and denitrification (Arce et al., 2014; Skoulikidis and Amaxidis, 2009; Skoulikidis et al., 2017b). In soils, mechanisms behind such biogeochemical bursts are mainly based on the disruption of organo-mineral complexes, understood as aggregates playing a significant role in nutrient sorption-desorption processes (Kinsman-Costello et al., 2016) and the release of intracellular components due to osmotic stress associated with a rapid rise in water potential, resulting in increased labile C and nutrient supply for remaining microorganisms (Birch, 1958; Butterly et al., 2009; Fierer et al., 2003; Griffiths and Birch, 1961).

The increase in water availability linked to pulses of nutrients and C can have multiple effects on microbial dynamics: (i) reactivation of a large number of dormant microbes (Kuzyakov and Blagodatskaya, 2015; Timoner et al., 2012), (ii) shifts in microbial community composition (Griffiths and Philippot, 2013; Stegen et al., 2016a), and (iii) increases in decomposition (Kuzyakov et al., 2000). In soils and DRBs, any increase in pore water content can favor the development of anaerobic habitats (McIntyre et al., 2009) and promote denitrification and emissions of N gas fluxes (Austin and Strauss, 2011; Gallo et al., 2014; Groffman and Bohlen, 1999). Yet, increases in pore water content can limit aerobic mineralization processes such as leaf litter decomposition driven by fungi (Mora-Gómez et al., 2015; Schlief and Mutz, 2011; but see Risse-Buhl et al., 2017). Models developed in desert soils describing the vertical mobilization and transformation of nutrients after rainfall (i.e.

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Trigger-Transfer-Reserve Pulse (TTRP); Belnap et al., 2005) would also apply to DRBs during rainfall as well as during early stages of flow resumption (Larned et al., 2010). In combination with the gradual change in DRB development, variability in water availability has great potential to shape DRB biogeochemistry. Thus, application of our conceptual framework should take into account the significant role played by punctuated changes in water availability in DRBs during dry phases.

4. Conclusions and future directions

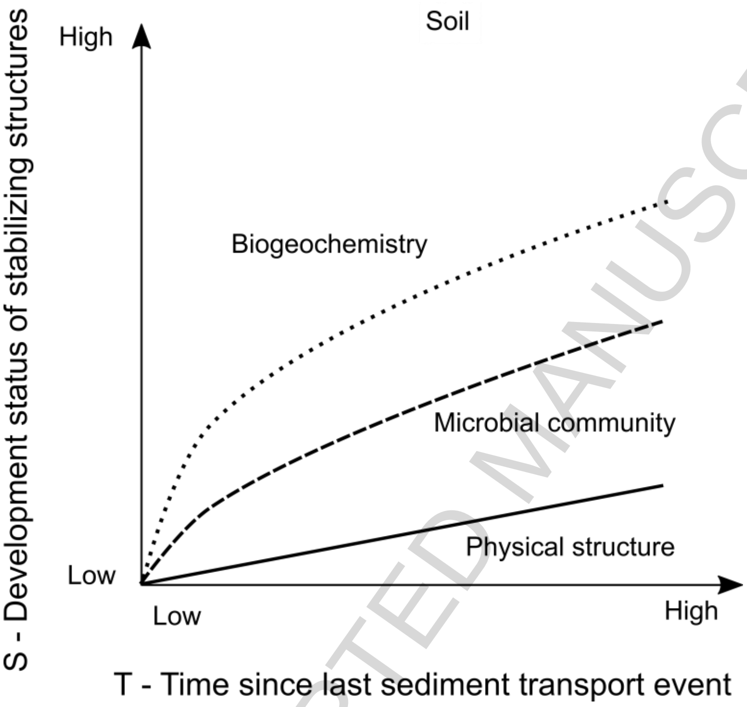

Figure 4. Conceptual framework indicating the degree of similarity in physical structure, microbial community and biogeochemistry of dry riverbeds (DRBs) of non-perennial watercourses (intermittent and ephemeral) with soils as a function of two main drivers: (T) time since the last sediment transport event, and (S) development status of stabilizing structures such as soil biocrusts or vascular plants.

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Expanding our initial conceptual framework (**Figure 1b**), in **Figure 4** we suggest that the driver T (time since last sediment transport event) modulated by the driver S (development status of stabilizing structures) triggers a series of changes in physical, microbial and biogeochemical dimensions of DRBs that move these habitats to a certain extent towards soils. Yet, the rate of change of each dimension is different (**Figure 4**). Among the descriptors examined in this paper, many physical

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features (e.g. horizons and aggregates) need far more time to develop than the relative short time periods between sediment transport events. In contrast, biogeochemical conditions in DRBs, generally more amenable to changes in response to environmental factors (e.g. water availability), can become similar to soils more rapidly (Romaní et al., 2017). Further, different structural and functional attributes can interplay and facilitate each other. For instance, the establishment and growth of terrestrial plants will favor the development of aggregates, at the same time creating habitat for specific terrestrial microorganisms.

Our review suggests that DRBS and soils may share key drivers/controlling factors of biogeochemical processes and their rates. The power of our conceptual model (**Figure 1b** and **Figure 4**) resides in summarizing the structural and functional changes that occur in DRBs towards their gradual development to soils. However, the application of the model requires consideration of concurrence, so that key drivers across climates and scales can be incorporated. For instance, while photodegradation plays an important role in arid regions, such a role can be of low relevance in temperate zones in forested catchments (del Campo and Gómez, 2016). The importance of concurrence is well reflected in the reverse pattern of vegetation observed in arid regions, where DRBs can sustain much more vegetation and OM than uphill soils compared to temperate ones (**Figure 1c ii** and **iii**; Scott et al., 2013).

Progress in understanding highly dynamic IRES has been limited by a lack of knowledge and empirical studies on dry phase dynamics (e.g. no data are available on net primary production for DRBs; **Table 2**). Part of this knowledge gap about IRES appears related to the fact that DRBs have been considered irrelevant for ecosystem functioning and traditionally ignored by freshwater scientists (Steward et al., 2012). As reported here, growing research in this direction clearly refutes this contention (e.g. Arce et al., 2014; Gómez-Gener et al., 2015; Merbt et al., 2016; von Schiller et al., 2014). Further, methodological limitations of approaches developed from and for fluvial biogeochemistry within an aquatic framework contributed to this functional overlook of DRBs.

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Our comparison of physical and biogeochemical properties between soils and DRBs reflects that DRBs exhibit both parallels and differences with terrestrial soils and share many mechanistic responses to environmental change. Parallels in drivers of biogeochemical processing can be highly dependent on climatic zone and landscape context (e.g. geomorphology, dominant biota). While drying-rewetting effects can be widely transferred to DBRs across biomes, the action of other drivers and constraints that influence biogeochemistry at regional scales (e.g. solar radiation, temperature, OM inputs) may not be easily transferable across regions. Thus, identifying primary controls of biogeochemical processes in soils is a first step to understand target controls predicting biogeochemical responses in DRBs in the same landscape.

On the other hand, we still ignore many aspects about how biotic assemblages (microbes, plants and animals), their drivers, dynamics and influence on biogeochemical activity could converge between DRBs and soils (Sabater et al., 2016; Sanchez-Montoya et al., 2017). Compared with soils, we found a paucity of studies examining biogeochemical aspects of DRBs and thus more research in DRB biogeochemistry must become a priority. Large-scale collaborative initiatives also are key opportunities to expand the knowledge of DRB biogeochemistry across biomes, for instance the 1000 Intermittent Rivers Project (https://1000_intermittent_rivers_project.irstea.fr) and the DryFlux GLEON initiative (http://www.ufz.de/dryflux/), the latter explicitly designed to estimate C emissions from concurrent DRBs and upland soils.

Our paper emphasizes the strong link between IRES and their catchments and stresses that IRES research allows the integration of terrestrial and aquatic disciplines to understand landscape biogeochemistry. Together with the recent empirical evidence on DRB biogeochemistry, the transfer of soil science also contributes to expand previous concepts developed to explain the general functioning of IRES. In their conceptual paper, Larned et al. (2010) contend that IRES function as punctuated longitudinal bioreactors of material transformation, featuring higher rates during inundated periods (or flowing sites) than during dry periods. We have seen, however, that DRBs, as soils, can support higher rates of certain biogeochemical processes such as aerobic CO_2 emissions and nitrification compared with flowing waters (Gómez-Gener et al., 2015; Merbt et al., 2016; von

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Schiller et al., 2015). We suggest that specific environmental requirements of target biogeochemical pathways should be considered when formulating predictions based on water fluctuations at the whole river scale.

It is worth noting here that a functional understanding of DRBs also is critical beyond the dry phase. For example an important biogeochemical effect of DRBs is the release and export of nutrients once flow resumes (Arce et al., 2014; Butturini et al., 2003; Gómez et al., 2012; Merbt et al., 2016; Skoulikidis and Amaxidis, 2009; Skoulikidis et al., 2017b). From a management perspective of water resources, DRBs must be viewed as an integral part of fluvial networks since what happens in them can greatly determine the nutrient status and ecosystem services in aquatic phases of downstream reaches.

We encourage freshwater biogeochemists to adopt the perspective and knowledge of soil science, a discipline with a long and consolidated trajectory, to carry out research on DRBs. Transferring field and laboratory approaches from soil science to mechanistically understand DRBs, as well as providing explanatory and merging models of biogeochemical fluxes that encompass aquatic and dry phases with surrounding soils will definitely enhance the understanding of the role of DRBs and IRES across temporal and spatial scales. Lastly, we expect this paper to reinforce the idea that merging concepts and perspectives from terrestrial and aquatic sciences, traditionally separate disciplines (Dollar et al., 2007), are necessary to gain a complete understanding of ecosystems where connections between terrestrial and aquatic elements are tight (Grimm et al., 2003), as demonstrated for IRES.

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Author contribution

MIA and CM-L assumed responsibility for the overall manuscript planning and coordination with support by DvS as working group coordinator. MIA and CM-L were responsible for section 1, 3.4 and 4 and further compiled and integrated all sections. MA lead and coordinated section 2. AMR and AF lead and coordinated section 3.1. AMR and NC lead and coordinated section 3.2. SB, EM and RG lead and coordinated section 3.3. GG was responsible for the art work. All authors commented on and contributed to revising draft versions.

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