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Additional Information

NICHE CONSTRUCTION WITHIN RIPARIAN CORRIDORS. PART II: THE UNEXPLORED ROLE OF POSITIVE INTRASPECIFIC INTERACTIONS IN *SALICACEAE* SPECIES

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Abstract

Within riparian corridors, *Salicaceae* trees and shrubs affect hydrogeomorphic processes and lead to the formation of wooded fluvial landforms. These trees form dense stands and enhance plant anchorage, as grouped plants are less prone to be uprooted than free-standing individuals. This also enhances their role as ecosystem engineers through the trapping of sediment, organic matter, and nutrients. The landform formation caused by these wooded biogeomorphic landforms probably represents a positive niche construction, which ultimately leads, through facilitative processes, to an improved capacity of the individual trees to survive, exploit resources, and reach sexual maturity in the interval between destructive floods. The facilitative effects of riparian vegetation are well established; however, the nature and intensity of biotic interactions among trees of the same species forming dense woody stands and constructing the niche remain unclear. Our hypothesis is that the niche construction process also comprises more direct intraspecific interactions, such as cooperation or altruism. Our aim in this paper is to propose an original theoretical framework for positive intraspecific interactions among riparian *Salicaceae* species operating from establishment to sexual maturity. Within this framework, we speculate that (i) positive intraspecific interactions among trees are maximized in dynamic river reaches; (ii) during establishment, intraspecific facilitation (or helping) occurs among trees and this leads to the maintenance of a dense stand that improves survival and growth because saplings protect each other from shear stress and scour; (iii) in addition to the improved capacity to trap mineral and organic matter, individuals that constitute the dense stand can cooperate to mutually support a mycorrhizal network that will connect plants, soil, and groundwater and influence nutrient transfer, cycling, and storage within the shared constructed niche; (iv) during post-establishment, roots form functional grafts between neighbouring trees to increase biomechanical and physiological anchorage as well as nutrient acquisition and exchange; and (v) these stands remain dense on alluvial bars until a threshold of landform construction and hydrogeomorphic disconnection is reached. At this last stage, intraspecific competition for resources (light and nutrients) increases, inducing a density reduction in the aerial stand (i.e., self-thinning), but root systems of altruistic

individuals could remain functional via root grafting. Finally, we suggest new methodological perspectives for testing our hypotheses related to the occurrence of positive intraspecific interactions among *Salicaceae* trees in fluvial landform and niche construction through *in situ* and *ex situ* experiments.

Keywords

Contents

1   Introduction

Within riparian corridors, *Salicaceae* species (poplars and willows; hereafter RSS) affect water flow and sediment dynamics (i.e., hydrogeomorphic processes). Biogeomorphic studies explicitly consider such *ecosystem engineer* effects (sensu Jones et al., 1994; terms in italic are defined in **Table 1**) of RSS and argue that these plants can significantly affect fluvial landform development and riparian community dynamics (Bendix and Hupp, 2000; Corenblit et al., 2007a, 2009; Gurnell, 2014). In biogeomorphic ecosystems, feedbacks between plants and geomorphic dynamics control ecosystem resistance and resilience (Corenblit et al., 2015; Eichel et al., 2016; Hortobágyi et al., 2017; Stallins and Corenblit, this press). The process of fluvial landform construction and related changes in habitat and biotic conditions is considered as a *positive niche construction* (sensu Odling-Smee et al., 2003), improving RSS anchorage, water/nutrient uptake and storage, as well as capacity to reach sexual maturity in the interval between destructive floods (Francis et al., 2009; Corenblit et al., 2014).

The theoretical usefulness and empirical significance of the niche construction theory has been proved (Matthews et al., 2014; Laland et al., 2016) after debates in the evolutionary biology community (Dawkins, 2004; Laland, 2004; Scott-Phillips et al., 2014; Laland et al., 2016). The niche construction theory has been adopted in several domains of evolutionary biology and ecology (Erwin, 2008; Post and Palkovacs, 2009). It was recently introduced into biogeomorphology and has been very stimulating in the description of ecoevolutionary feedbacks between organisms and their geomorphic environment (Stallins, 2006; Corenblit et al., 2007b; Phillips, 2016). However, from the biogeomorphic perspective, niche construction remains a hypothesis to be tested *in* and *ex situ*. Corenblit et al. (2014) pointed out that engineer organisms acting on the geomorphic dimensions of their niche may be considered niche constructors if the following three criteria are met (see also Matthews et al., 2014): (i) the organisms must significantly modify their geomorphic environment; (ii) these modifications must influence selection pressures on at least one recipient organism; and (iii) there must be an evolutionary response (i.e., change in the frequency of DNA sequences in a population, from one generation to the next) caused by the geomorphic modification in at least one recipient population. We believe that the effects of RSS on fluvial landforms (i.e.,

criterion i) are well established (Gurnell, 2014), but that criteria (ii) and (iii) remain to be proved and should be studied in relation with the question of why RSS are so successful in constructing their niche within riparian corridors. Besides the specific response traits of RSS to hydrogeomorphic constraints (Karrenberg et al., 2002; Lytle and Poff, 2004; Bornette et al., 2008), we hypothesize that the nature and intensity of biotic interactions among RSS that form dense stands are keys to understanding the reasons for the efficiency of RSS in constructing their niche within riparian corridors. Plants exhibit *competitive traits* that grant them better access to resources (Cahill and McNickle, 2011), thus a negative relationship between population density and individual fitness is commonly admitted. However, the *stress gradient hypothesis* (Bertness and Callaway, 1994) predicts that interactions among plants shift from *competition* to *facilitation* as environmental *disturbances* and constraints increase (see also Brooker and Callaghan, 1998). Facilitation enhances diversity within such environments by expanding the *realized niche* of species (see also Crain and Bertness, 2006; Brooker et al., 2008; He et al., 2013). In particular, Bruno et al. (2003) suggested that plant survival can be positively related to population density within harsh environments. These authors pointed out that environmental constraints can control the balance between cost and benefit of living under a high or low population density. Under harsh physical conditions, high stem density enhances individual survival if neighbouring individuals buffer each other from physical constrains and improve local habitat conditions (facilitation). Within riparian corridors, the hydrogeomorphic flow regime (i.e., frequency, magnitude, duration, and timing of floods; Poff et al., 1997) modulates resource availability but also disturbance and *stress* and therefore the nature and intensity of interactions among riparian plants. Riparian corridors are particularly prone to shifts in ecological strategies of organisms along the upstream-downstream gradient of energy (Vannote et al., 1980; Bornette et al., 2008) and in particular on the predominant interactions among plants, i.e., from positive to negative interactions (Corenblit et al., 2007a). However, despite the recognition of interspecific facilitation in riparian vegetation development and organisation, *positive intraspecific interactions* among RSS have, as far as we know, not been studied in detail. Such interactions could comprise an unexpected set of underlying niche construction mechanisms.

Based on a review of positive intraspecific interactions among terrestrial plants as well as their modalities and means, our aim is to propose an original theoretical framework of fluvial landform construction based on positive intraspecific interactions among RSS from *establishment* (first three years; Cooper et al., 1999) to sexual maturity, i.e., in the first 10 years of growth (**Table 2**). Here we shall present the three possible types of positive intraspecific interactions (i.e., facilitation, cooperation, and altruism). We suggest that these positive intraspecific interactions among RSS occur in dynamic river reaches with a contrasting hydrologic regime. In such a context, the maintenance of a dense RSS stand improves survival and growth because multiple individuals (i) buffer shear stress more efficiently and (ii) act together to build a shared niche for the anchorage and uptake, storage, and exchange of water and nutrients. We stress the fact that the proposed framework is speculative. It is mainly based on knowledge taken from terrestrial plant studies as we are not aware of any studies related to the topic within the riparian context. The goal of the article is to persuade the biogeomorphic community to use the theoretical framework of positive intraspecific interactions to test the hypothesis of RSS niche construction. In order to stimulate future research, we describe possible mechanisms of these positive interactions and propose methodological perspectives related to our research hypotheses.

Table 1. Glossary of biological and ecological terms used in this paper.

Term	Definition	Reference
Arbuscular mycorrhiza	Mycorrhiza where the fungus penetrates the cortical cells of the roots of vascular plants.	Rillig and Mummey (2006)
Altruism	Positive intraspecific interaction in which helping is costly to the helper.	Lehmann and Keller (2006)
Cheater	An individual taking the benefits while not providing help and thus avoiding the costs of the interaction.	Hamilton (1964)
Clonal propagation	A process of colonization by genetically identical plants that arises without the production of seeds or spores.	Rood et al. (1994)
Colonization	Period when new individuals colonize a new habitat or are added to an existing population.	Eriksson and Ehrlén (2008)
Competition	Mutually detrimental interaction between individuals.	Hardin (1960); Sahney et al. (2010)
Competitive traits	Morphological, biomechanical, physiological or phenological attributes of the plant enhancing competitive ability for colonization, resource acquisition and reproduction.	Cahill and McNickle (2011)
Cooperation	Positive intraspecific interaction that is beneficial to both the helper and the helped individual.	Axelrod and Hamilton (1981)
Disturbance	Environmental or biological event affecting the physical integrity of organisms and habitats.	Rykiel (1985); Grime et al. (2014)
Ecosystem engineer	Organisms that create, modify or maintain habitats (or microhabitats) by causing physical state changes in biotic and abiotic materials and that, directly or indirectly, modulate the availability of resources to other species.	Jones et al. (1994, 1997); Gutiérrez et al. (2003)
Ectomycorrhizal fungi	Fungi that form a symbiotic relationship with a plant via a sheath around the root tip of the plant. The fungus forms hyphae that penetrate the plant root structure (Hartig network).	Piotrowski et al. (2008)
Establishment	Stage of vegetation development when seedlings become permanently established in a habitat during the first growing seasons.	Cooper et al. (1999)
Inter- and intraspecific facilitation	Indirect positive interspecific (or intraspecific) interaction at the same trophic level and where at least one of the protagonists' benefits.	Bronstein (2009); McIntire and Fajardo (2014); Dudley (2015)
Green beard effect	A gene for selective altruism can be favoured by (natural) selection if the altruism is primarily directed towards other individuals who share the gene and exhibit a perceptible trait (the hypothetical 'green beard'). If this trait is recognised by others and leads to preferential treatment of individuals with the trait, the trait and the altruistic behaviour will increase in the population.	Dawkins (1976)
Helping	Collective term for cooperation and altruism.	Lehmann and Keller (2006)

Kin selection	Evolutionary strategy that favours the reproductive success of an organism's relatives, even at cost of the organism's own survival and reproduction. If interactants are sufficiently closely related, altruism can benefit reproduction of the set of genes they share despite losses of direct fitness by the individual altruist.	Axelord and Hamilton (1981)
Niche construction	The process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other's niches. Niche construction may result in changes in one or more environmental constraints acting on the populations. Niche-constructing organisms may either alter the environmental constraints of their own population, of other species, or of both.	Odling-Smee et al. (2003)
Mutualism	Positive interaction between species from different trophic levels in which both species benefit, i.e., the interspecific equivalent of cooperation.	Bronstein (1994)
Mycorrhiza (pl. mycorrhizae)	A symbiotic association between beneficial fungi and roots of a vascular plant.	Kirk et al. (2001)
Opportunistic plant strategy	Colonization strategy involving short-lived plants with high reproductive and dispersal capacities.	Grime et al. (2014)
Positive intraspecific interactions	Set of interactions between plants that can lead to an improved capacity of survival and reproduction of the individuals constituting a population. They include facilitation, cooperation and altruism.	Lehmann and Keller (2006); Dudley (2015)
Positive niche construction	Niche-constructing actions that, on average, will increase the survival and reproduction of the niche-constructing organisms.	Odling-Smee et al. (2003)
Realized niche	The part of the environmental parameter space (the niche) that is effectively occupied by an organism in relation with the limiting (e.g., competition) or enhancing (e.g., facilitation) factors present in the ecosystem.	Connell (1961); Bruno et al. (2003)
Reciprocal altruism	Positive intraspecific interaction requiring repeated interactions between the same individuals and in which both individuals benefit.	Axelrod and Hamilton (1981)
Recruitment	Early population phase corresponding to the development of seedlings and saplings from primary or secondary dispersal following habitat disturbance.	Mahoney and Rood (1998)
Root grafting	Anastomosis or fusion between roots of compatible neighbouring plants.	Graham and Bormann (1966); Tarroux and DesRochers (2010)
Stress	Predictable environmental event (e.g., drought) or habitat property (e.g., saltiness) inducing physiological changes and/or ecological specialization in living organisms.	Grime et al. (2014)
Stress gradient hypothesis	Model predicting that the balance between facilitation and competition vary along abiotic stress gradients. Facilitation is expected to be the dominant interaction in conditions where abiotic stress is high.	Bertness and Callaway (1994); Bruno et al. (2003)

Table 2. Nature of interactions and processes related to the hypotheses of RSS intraspecific interactions.[a]

Mechanism of positive biotic interaction	Biotic process		Cost	Direct benefit	Indirect benefits	Cheating mechanism
Niche construction (environment modification)	Facilitation		None	None	Protective effect of the neighbours against shear stress and uprooting	None
					Construction of a mutual resource (fine sediment, organic matter, nutrients)	None
Mycorrhiza sharing	Facilitation/ Cooperation		Nutrients provided to support the mycorrhizal community	Increased access to nutrients Increased substrate stability to water flow	Construction of a mutual resource (mycorrhizal network) Increased survival and reproduction of related individuals (kin selection)	Unequal redistribution of nutrients and water taken up by the mycorrhizae and unequal provisioning of the mycorrhizal community
Root grafting	Cooperation		Construction of root connections Provision of nutrients and photosynthates to connected trees	Protection against shear stress and uprooting Protection against shear stress and uprooting	Increased survival and reproduction of related individuals (kin selection)	Unequal redistribution of sap between grafted trees
Crown dieback	Altruism	Performer	Construction of root connections Loss of photosynthesis and sexual reproduction	None	Increased survival and reproduction of related individuals (kin selection)	None
		Recipient	Construction of root connections Provision of nutrients and photosynthates to the connected crownless tree	Increased access to water and nutrients		No redistribution of elaborated sap to the crownless grafted trees

[a] We detail the costs and benefits corresponding to each type of interaction, separating the direct benefits, i.e., the benefits that are the direct outcome of the interaction (e.g., provision of nutrients), from the indirect benefits that are a by-product of the interaction (facilitation) or an intergenerational effect (kin selection). Intraspecific facilitation and cooperation are symmetrical interactions as they involve similar individuals in reciprocal interaction. Altruism, however, is an asymmetrical interaction and we describe the costs and benefits of each interacting individual, the performer of the altruistic behaviour and the recipient.

2   Positive niche construction by riparian *Salicaceae* species (RSS)

We define positive niche construction by RSS as 'actions on geomorphic, habitat, and biotic dimensions of their niche that will increase their survival and reproduction' (for a detailed description see Corenblit et al., 2009, 2014). The theory of niche construction was based on the idea that selection pressures can be changed in directional ways by engineer organisms. The directionality of change in selection pressures makes niche construction an evolutionary process per se (Scott-Phillips et al., 2014). Corenblit et al. (2009) suggested that the actions of RSS on their riparian environment ultimately increased their fitness, which implies an adaptive complementarity between RSS traits and the hydrogeomorphic environment. Any genetically determined trait that modifies the geomorphic environment in a direction suitable for the engineer plant will be favoured in a selective context. Thus, constructed fluvial landforms can be considered to be extended expressions ('extended phenotype' sensu Dawkins, 1982) of their genotype. The authors proposed the concept of *biogeomorphic life cycle* to describe the adaptive nature of reciprocal actions between different life cycle stages and co-occurring directed changes in the geomorphic environment controlled by the RRS (Corenblit et al., 2014). Stallins and Corenblit (this press) suggested that equivalent directional biogeomorphic feedbacks between plants and geomorphology also occur within coastal dune ecosystems.

The key question of this paper is: are free-standing RSS in dynamic river reaches able to construct their niche alone? When exposed to floods, free-standing RSS saplings are most generally subjected to uprooting or injuries caused by water flow, bedload sediment transport, and erosion. When they are not uprooted, they are regularly damaged during large floods but can still affect landform dynamics locally by creating an obstacle mark (Rodrigues et al., 2007; Euler et al., 2014) and by forming clones (Gomand Rood, 1999a). However, they generally do not reach sexual maturity in significant proportions (Corenblit et al., 2014). Water that flows through a vegetated patch composed of several plants is subject to much more drag and roughness resistance. Flow resistance induced by RSS decreases flow transport capacity, which leads to uprooting and an increase in fine sediment deposition within the vegetated patch (Chen et al., 2012a) compared to the bare, nonvegetated local environment (Corenblit et al., 2016a). Such fine sediment deposition within vegetated patches is the main process to sustain fluvial landform construction and enhance the progressive sheltering and disconnection of vegetation from hydrogeomorphic disturbances (Corenblit et al., 2016b). Several flume experiments showed that not only flow and sediment dynamics control vegetation density but vegetation density is also a key parameter in the control of flow resistance and sediment deposition (Righetti, 2008; Aberle and Järvelä, 2013). Flow resistance and the capacity to trap fine sediment seem to be positively correlated with increasing stem density (Corenblit et al., 2016b). This would mean that within dynamic river reaches RSS would benefit from growing in a dense stand composed of several individuals that interact.

3   Types of positive intraspecific interactions in plants

Our hypothesis of a positive niche construction enhanced by positive intraspecific interactions is based on the following considerations. First, plants are able to sense their physical and biological environments in very subtle and integrative ways and provide adapted responses to complex external stimuli (Vandenbussche et al., 2005; Cahill and McNickle, 2011; Osakabe et al., 2013; Moulia et al., 2015). Since Baldwin and Schultz (1983) demonstrated that intact trees are able to activate their defence systems when exposed to herbivore-damaged trees, an increasing number of studies have shown that, in addition to their responses to physical factors, plants also communicate and interact by using airborne (Karban et al., 2014) and belowground (Biedrzycki et al., 2010) chemical signals. Second, plants are able to recognize their neighbours and respond accordingly (e.g., Callaway, 2002; Murphy and Dudley, 2009; Biedrzycki and Bais, 2010; Chen et al., 2012b; File et al., 2012a; Dudley et al., 2013; Gorelick and Marler, 2014; Semchenko et al., 2014; Gagliano, 2015).

Three types of positive intraspecific interactions can be described depending on the global outcome (i.e., the cost-benefit balance) for each individual (**Table 2**): First, the interaction can be beneficial for one and neutral for the other individual (*intraspecific facilitation*). Intraspecific facilitation is an indirect interaction by which, similarly to interspecific facilitation, the sheer presence of an individual modifies the environment of its neighbours (McIntire

and Fajardo, 2014). Second, the interaction can be beneficial for both (*cooperation*, i.e., the intraspecific equivalent of *mutualism*); and third, it can be beneficial for one and detrimental for the other individual (*altruism*).

Cooperation and altruism (collectively referred to as *helping*; Lehmann and Keller, 2006) are one of the enduring puzzles in biology and the social sciences because the classical theory of natural selection cannot explain the evolution of a character that, on average, is disadvantageous to the individual possessing it (Hamilton, 1964). Even in conditions that are not harmful to the individual performing a cooperative act, the maintenance of cooperation is a puzzle as any *cheater* would be favoured and would thus increase in frequency across generations until the population comprises only cheaters.

At least one of the following conditions needs to be fulfilled for the evolution (in its Darwinian sense) of cooperation and altruism (Lehmann and Keller, 2006): (i) no cost to the individual performing a cooperative act; (ii) repeated reciprocal interactions in which both individuals behave altruistically (*reciprocal altruism*; Axelrod and Hamilton, 1981); (iii) preferential interactions among related individuals (*kin selection*; Hamilton, 1964); and (iv) genetic correlation between genes coding for altruism and phenotypic traits that can be identified (*green beard effect*; Dawkins, 1976). The first condition corresponds to intraspecific facilitation. Reciprocal altruism requires a sufficiently high probability of repeated encounters between individuals; this condition does not, however, explain how cooperation first occurs and is selected in a population of competitors. Kin selection is based on Hamilton's rule of inclusive fitness, in which cooperation among relatives (i.e., individuals that share a large fraction of their genes) enables their common genes to be passed on to subsequent generations (Hamilton, 1963), even at a net cost to the cooperator; any cheater will lose from not cooperating as this will decrease the fraction of common genes passed on. The green beard effect is a case of kin selection restricted to a few traits (the cooperation and the identification traits); cheating will uncouple the cooperation and identification traits and lead to a loss of cooperation (Lehmann and Keller, 2006). Consequently, helping behaviours or traits should mostly be found among kin.

Several examples of positive intraspecific interactions among kin have been provided for terrestrial plants. Dudley and File (2007) showed that *Cakile edentula* invested more energy into root biomass (a competitive trait) in pots shared by groups of strangers than in pots shared by groups of close relatives (see also Bhatt et al., 2011). Groups of close relatives can therefore allocate more energy to aboveground biomass and thus potentially to higher seed production. Murphy and Dudley (2009) showed that *Impatiens pallida* plants decreased their aboveground biomass (stems and leaves) when surrounded by close relatives compared to nonrelated individuals, thus becoming less competitive (more cooperative) regarding access to light. Biedrzycki et al. (2011) demonstrated that *Arabidopsis thaliana* plants modulated competition by adjusting root development in the presence of related vs. nonrelated individuals. Lepik et al. (2012) found that the response to neighbours was species-dependent with only species that have a high probability to grow with siblings in the field, e.g., species that have low seed dispersal capacities, showing reduced competitive traits when confronted with related individuals. However, these experiments did not last until reproduction and thus did not estimate fitness, which is usually measured by the reproductive output. On the other hand, intraspecific facilitation was described for seedlings and grown trees of *Nothofagus pumilio* in central Patagonia where winds are very strong (Fajardo and McIntire, 2011; McIntire and Fajardo, 2011). Trees of this species cooperate in resource acquisition and against uprooting by way of stem fusion at the edge of second-growth forests where wind stress is most intense (Fajardo and McIntire, 2010). This cooperation mostly occurs among highly related trees and is the result of a selection process in favour of related trees in groups of seedlings (probably through kin selection) (Till-Bottraud et al., 2012; Fajardo et al., 2016).

Intraspecific facilitation has been observed in riparian corridors, e.g., on the meandering Garonne River, France (Corenblit et al., 2016b), and on the island-braided Tagliamento River, Italy (Gurnell et al., 2005), where RSS establish in high density stands, protect each other from hydrogeomorphic constraints, and build fluvial islands and floodplains. Similarly to what was observed in *N. pumilio*, we assume that cooperation or altruism can be found in disturbed and stressed riparian forests, preferentially occurring among highly related trees.

4 Where should positive intraspecific interactions occur along the river upstream-downstream energy gradient and why there?

Within riparian corridors, a shift from facilitation to competition is found along the upstream-downstream gradient of energy (longitudinal dimension) and the channel-floodplain gradient of hydrological connectivity (transverse dimension). Shear stress and erosion increase upstream and closer to the channel (Bornette et al., 2008), imposing mechanical and physiological limits beyond which woody vegetation cannot establish (Corenblit et al., 2015). In confined (torrential, high energy) river reaches, *opportunistic plant strategies* dominate, while in sinuous and anastomosing (piedmont, low energy) river reaches, competitive strategies dominate throughout the entire riparian corridor (**Figure 1**). In the transition between torrential and piedmont reaches, where braided river reaches occur, RSS mostly adopt a strategy based on *clonal propagation* from woody debris, tree fragments, and suckers that support the *colonization* of exposed gravel bars (Rood et al., 1994; Stromberg et al., 1997; Arens et al., 1998; Gom and Rood, 1999b; Barsoum et al., 2004).
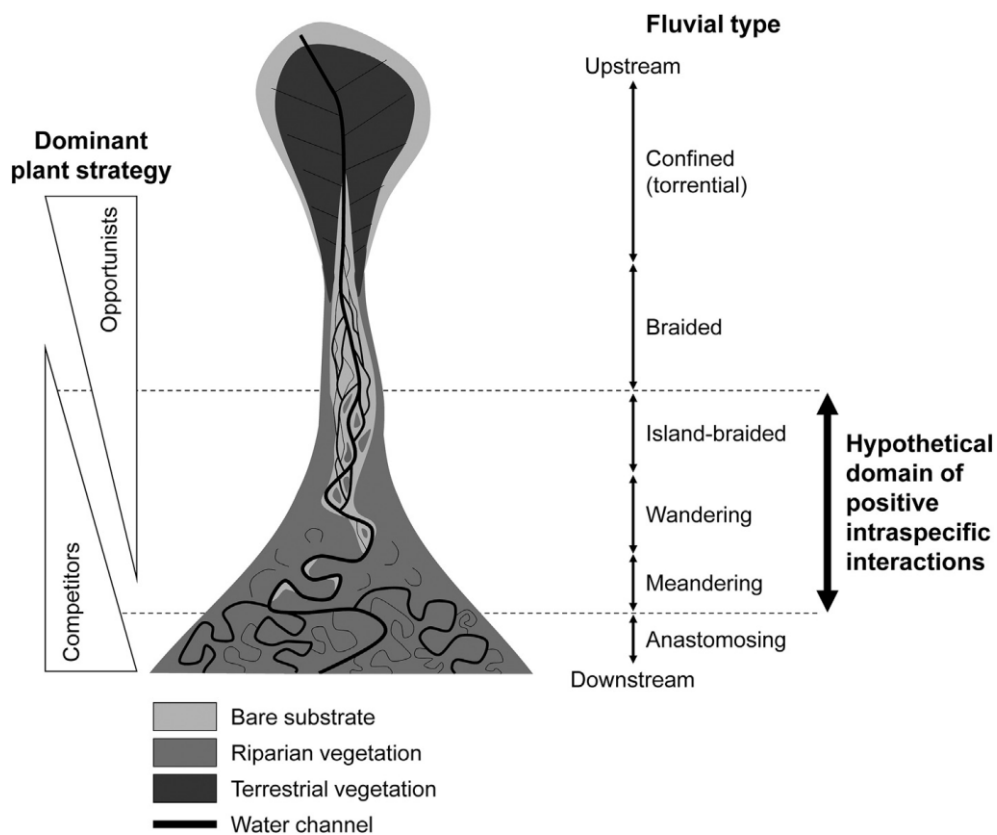

Figure 1. Hypothetical domain of positive intraspecific interactions along the upstream-downstream longitudinal gradient of energy of a river.

Following the stress gradient hypothesis, we suggest that positive intraspecific interactions are likely to be maximized among RSS when they grow in dense stands where hydrodynamic forces are neither too intense nor too weak, e.g., on exposed alluvial bars and river margins within a longitudinal schematical sequence of island-braided, wandering, and meandering river reaches (**Figure 1**). We acknowledge that this idealized continuum of geomorphic settings along the upstream-downstream gradient of energy is in reality more complex and disrupted by discontinuities; but in general terms, when RSS are grouped during establishment within a dense stand, seedlings and saplings can improve their survival and growth because individuals protect each other from shear stress and uprooting, i.e., show intraspecific facilitation or cooperation. Corenblit et al. (2016b) observed that the density of *Populus nigra* individuals on the meandering Garonne River in France remained high on alluvial bars until a threshold of landform construction and hydrogeomorphic disconnection was reached. In the wandering Tech River, France,

dense herbaceous and RSS sapling mats resisted erosion and promoted substrate stability during annual floods; conversely, similar vegetation mats with a low plant density tended to be eroded (Corenblit et al., 2009).

5   Mycorrhizal network: Mutual support by joint niche construction involving matter trapping

The RSS individuals protecting each other from shear stress and uprooting within a dense seedling and sapling stand construct fluvial landforms by efficiently trapping fine mineral and organic matter that buffers stress related to moisture content, low nutrient availability and heat during summer (**Figure 2A–C**, **Figure 3A–C**) (Tabacchi et al., 2000). Within only a few years, they build a biogeomorphic unit at the patch scale in the form of wooded fluvial islands, benches, and floodplains with an embryo soil and improved habitat conditions (**Figure 2B–F**, **Figure 3B–F**) (Corenblit et al., 2009, 2016a; Gurnell, 2014; Bätz et al., 2015). Successive fine sediment and allochthonous and autochthonous organic matter deposition raises the volume and quality of the substrate that can be explored and exploited for anchorage and resource acquisition (**Figure 2E**, **Figure 3E**) (Bätz et al., 2015). These two functions are performed by adventitious roots that RSS develop rapidly and systematically in each new fine sediment layer (Corenblit et al., 2014).
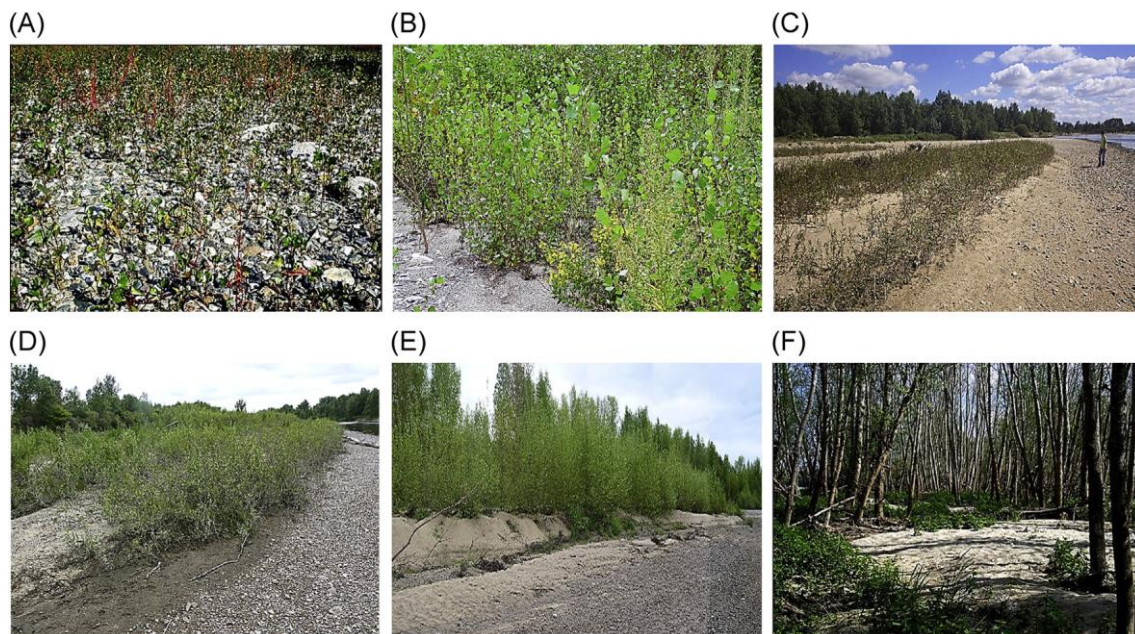

Figure 2. Illustration of different steps from establishment to sexual maturity of riparian *Salicaceae* species and related effect on fluvial landform construction: (A) *Populus nigra* seedling recruitment on a gravel bed of the Tech River, France (photo: D. Corenblit); (B) dense one year-old saplings mat in the Tech River (photo: D. Corenblit); (C) dense saplings mats of *Salix alba* (D) in the Allier River, France (photo: B. Hortobágyi), that at this stage are able to trap considerable amounts of fine sediments leading to the formation of pioneer islands within the river active tract; (E) effect of a dense cohort four years old of *P. nigra* on the construction of an elongated pioneer island within the active tract of the Allier River (photo: B. Hortobágyi); (F) stabilisation of a wooded bench within the river channel of the Garonne River, France, 15 years after recruitment (photo: L. Lambs).

In addition to their improved capacity to trap mineral and organic matter, RSS within dense stands that construct their niche together can mutually support a network of *mycorrhizae*. A large diversity of terrestrial plant species is able to exchange water, carbon, nitrogen, and phosphorus via mycelia (Brownlee et al., 1983; Francis and Read, 1984; Allen, 1991; Simard et al., 1997; Rillig and Mummey, 2006; Gonneau et al., 2014). Within riparian corridors, many RSS form an extensive rhizosphere influenced by root exudates and associated symbiotic mycorrhiza (Doty et al., 2005; Beauchamp et al., 2006; Gryta et al., 2006; Piotrowski et al., 2008).
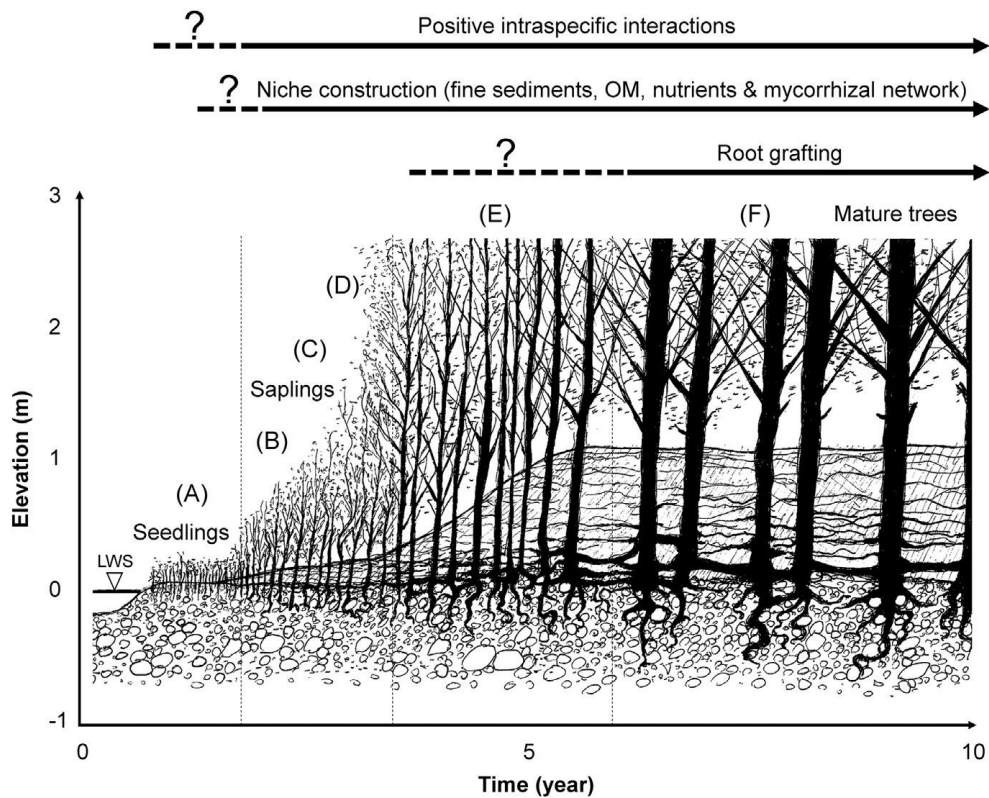
Figure 3. Hypothetical spatiotemporal model of niche construction of riparian *Salicaceae* species and related biological processes during establishment (i.e., first 3 years) and post-establishment until sexual maturity (3 to 10 years). The different steps from establishment to sexual maturity illustrated in **Figure 2A–F** are mentioned in this figure using the same letters. LWS: low water stage.

Mycorrhizal communities within riparian contexts have shown a characteristic shift from *arbuscular mycorrhiza* at the early stage to *ectomycorrhizal fungi* at the mature stage of riparian forest development (Gardes et al., 2003; Gryta et al., 2006; Piotrowski et al., 2008). At an early stage, ruderal arbuscular mycorrhiza (e.g., *Tricholoma scalpturatum*) enhance the connection between seedlings and favour Connected individuals by affecting phosphorus cycling and by storing carbon (Rillig and Mummey, 2006). Later successional mycorrhizae (e.g., *T. populinum* clones) have a competitive strategy that enhance their local persistence and interaction with their hosts. On the Tagliamento River, Italy, Harner et al. (2011) studied whether not only the type but also the quantity of arbuscular mycorrhiza changed during the sequence of biogeomorphic development within the active tract from a pioneer to an established fluvial island. The authors observed that the different stages had similar hyphal (~860 cm cm^{-3}) and colonized root lengths (~3 cm cm^{-3}). However, spore quantity increased from initial depositional (3.5 ± 0.9 (±SE) cm^{-3}), to pioneer (17 ± 6.1 cm^{-3}), and to established (32 ± 6.3 cm^{-3}) fluvial islands. Harner et al. (2011) suggested that mycorrhiza probably connect riparian plants, soil, and groundwater and influence nutrient transfer, cycling, and storage in the shared constructed niche. Mardhiah et al. (2016) used a greenhouse experiment to show that arbuscular mycorrhiza related to *Achillea millefolium* enhanced soil resistance to erosion by surface water flow. The authors observed that soil loss was affected by the combined effect of roots and arbuscular mycorrhiza. They identified the unique effect of arbuscular mycorrhiza hyphal length that reduced soil erosion, highlighting a potential significant repercussion on landform stability and niche construction.

All this suggests that in riparian corridors plant-fungi mutualism may act in combination with cooperation among RSS to sustain a mycorrhizal community. The mutualism provides a better access to resources, while cooperation among trees allows a large fungal population to stabilize and to share resources among different individuals. In this system, a cheater that takes fungal resources without sharing its own nutrients would grow faster. However, File et al. (2012b) showed that siblings of *Ambrosia artemisiifolia* had a larger mycorrhizal network and root colonization compared to strangers, which led to a higher amount of leaf nitrogen and reduced injuries caused by pathogens. This indicates a reduced incentive to cheat when networks are established by kin.

6 Root grafting: Improvement of water and nutrient sharing and anchorage within the constructed niche

We define post-establishment (close to 10 years; **Figure 2F**, **Figure 3F**) as the phase when RSS have significantly transformed their niche. At this stage, fluvial wooded islands and floodplains can be well developed and they are less exposed to recurrent floods because of a reduced hydrological connection to the bankfull channel. The RSS have also expanded their roots and rhizosphere in the sediment deposits and developed a tall canopy that enables them to improve resource acquisition. But at this stage RSS still remain exposed to large floods and can occasionally suffer from abrupt water drops in the sediments during droughts and low flow periods (Scott et al., 1999, 2000; Rood et al., 2000). We suggest that functional natural *root grafting* between neighbouring RSS at this stage may be a form of helping (cooperation or altruism) that improves resistance and resilience of trees (**Figure 2F**, **Figure 3F**). Lev-Yadun (2011) reviewed the reasons why trees should have root grafts and suggested that the benefits extend beyond the transfer of water, mineral, and carbohydrates and comprise an improved mechanical resistance in flooded and windy environments.

Since the publication of the foundation papers on natural root grafting between trees by Beddie (1941), Bormann and Graham (1959), and Graham and Bormann (1966), a lot of research has highlighted that this process commonly occurs in many species (Fraser et al., 2006; Tarroux and DesRochers, 2010, 2011; Tarroux et al., 2010, 2014). Lev-Yadun (2011) pointed out that grafts do not appear until a tree is large enough to have roots that are sufficiently thick to graft. For example, Fraser et al. (2005) reported that *Pinus contorta* show root grafts when their roots reach a diameter of 50 mm. However, these observations still need to be calibrated by species, in particular in the riparian context.

Root grafting occurs when root tissues from one tree are inserted into the tissues of another in such a way that the vascular tissues merge and the trees can thus exchange water and nutrients (Graham and Bormann, 1966) (**Figure 4**). The use of a shared root network allows the trees to optimise the use of resources by redistributing them, which leads to more growth, a better resistance to stress factors affecting resource acquisition, and an improved resilience. Initially, root grafting is a highly energy-consuming process, but in the long term it is beneficial to the growth of certain trees in the population. Using dendroecological techniques, Tarroux and DesRochers (2011) showed that during the period of root graft formation, *Pinus banksiana* trees tended to reduce their radial growth, which then increased once the roots were grafted. Root grafts could thus be a form of cooperation beneficial to all individuals involved. Fraser et al. (2006) showed that carbohydrate translocation mediated by root grafts between *Pinus contorta* trees allowed them to persist while nongrafted trees were outcompeted and died. Jelínková et al. (2009) noted that root grafting within and between clones of *Populus tremuloides* led to the formation of large (covering tens to hundreds of m²), physiologically functional, resistant units.

Within dynamic river reaches, exposure to mechanical constraints imposed by floods can have lethal effects on RSS. Also, resource distribution (water and nutrients) is generally heterogeneous and root grafts might represent biomechanical and physiological advantages for nutrient acquisition and anchorage. Field observations in riparian corridors indicated that RSS are able to form root grafts with a morphological fusion between two or more roots of originally distinct trees. Within the island-braided section of the Tagliamento River, Italy, Holloway et al. (2017) observed that complex root systems of poplars composed of buried stems, shoots, and adventitious roots of different individuals were sometimes grafted. The occurrence of natural root grafts between distinct individuals of *Populus nigra* has been observed during field investigations along the banks of the Garonne and Allier Rivers, France (unpublished field observations by the authors). A prospective anatomical analysis of root grafts from samples collected on the Allier River suggests a functional (i.e., leading to water and nutrient translocation) fusion between the conducting tissues of two distinct, connected *P. nigra* (**Figure 4**). We suggest that interindividual exchanges through root grafts will more likely occur during the post-establishment phase (i.e., 3 to 10 years after *recruitment*) between spatially close trees (at most a few meters apart), i.e., in areas where roots are the most abundant (**Figure 2E–F**, **Figure 3E–F**).
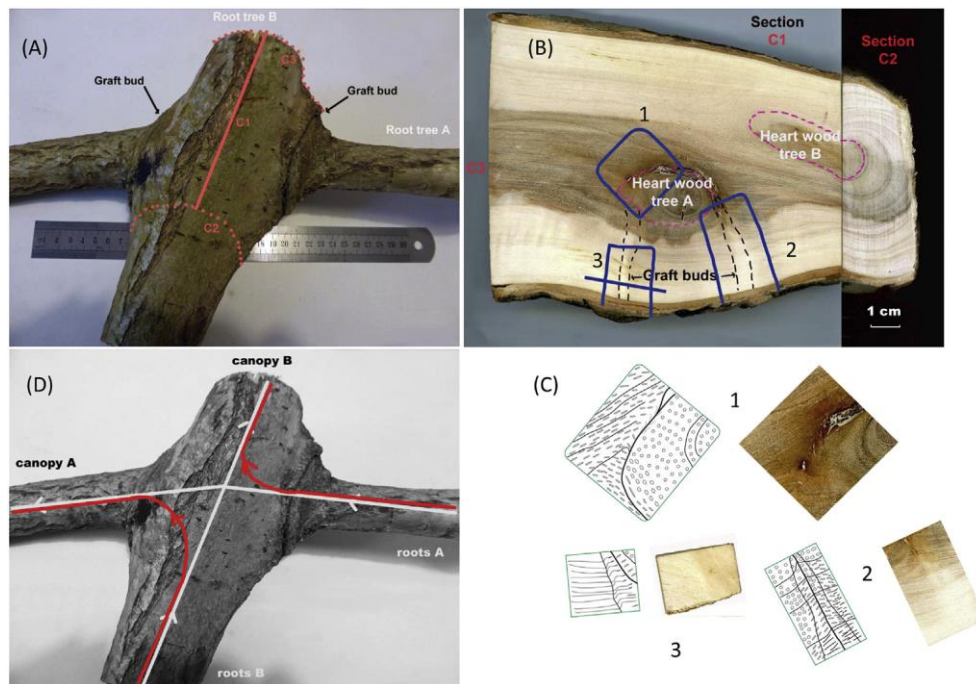
Figure 4. Anatomy of a root graft section between two distinct mature individuals of *Populus nigra* L. collected in the riparian corridor of the Allier River, France (46°24'58.22" N; 3°19'41.42"E). The two individuals with a height of 10 m were located at a distance of 0.5 m between each root collar on a river bank 3 m above a secondary channel. (A) Photo of the grafted roots, with root of tree A (diameter 3–4 cm) disposed horizontally and root of tree B (diameter 6–7 cm) disposed vertically. In order to analyse the impact of grafting on wood anatomy, the grafted roots were sawn along the C1, C2, and C3 axes. (B) The C1–C3 sections were sanded using successive coarse and fine sandpapers (finest: 1200 grift) and scanned at high resolution (720 and 1200 dpi). The two heart woods (delineated in pink on the photograph) were visually identifiable. In order to observe and understand wood vessel imbrications between the two roots, three subsamples (delineated in blue) were collected: sample 1 from the heart wood of tree A (horizontal plane), sample 2 from the graft bud on section C2 (horizontal plane), and sample 3 from the graft bud on section C3 (vertical plane). (C) The three samples were observed under a binocular microscope (Nikon SMZ 1500). Schematic anatomic representations of vessel sections (delineated in green) were drawn as seen from the binocular observations in order to simplify the information related to wood vessel orientation: circles correspond to a transverse vessel cross section view related to tree A; elongated ellipses correspond to an oblique to longitudinal vessel cross section view related to tree B. Sap exchange may be operational where vessels of tree A and tree B roots tend to be parallel. (D) In white, individual xylem sap flux direction of both roots from the substrate to the canopy; in red, possible diversion of sap because of root grafting as suggested by the structure of the vessels.

7   Altruistic behaviour during the post-establishment phase within the stabilized niche?

The benefits of a high stem density from establishment to sexual maturity (**Figure 2**, **Figure 3**) within dynamic river reaches (island-braided, wandering and meandering) have been described above. However, intraspecific competition possibly increases with plant growth, in particular where the exposure to hydrogeomorphic disturbance decreases while the niche is being constructed (i.e., related to sediment accretion and consequently to a topographic rise) (**Figure 2F**, **Figure 3F**). During RSS post-establishment a temporal shift in the trade-off between the advantages and the costs of a high stem density is therefore possible: on the one hand, the effect of tree survival increase, better resource trapping, habitat conditions improvement, and landform stabilisation; and on the other hand, the intraspecific competition for resources increases within the stabilized environment, which triggers the natural tendency to self-thin.

On the Garonne River, France, Corenblit et al. (2016b) noted that within dense post-pioneer riparian cohorts of *P. nigra* disconnected from annual floods, many stems, mainly the ones with a diameter b 5 cm, died or broke easily during large floods (see also Corenblit et al., 2014). The *P. nigra* stem density drastically and rapidly decreases after the first five post-colonization years, thus leaving more space for the development of the tall competitive stems on the aggraded and stabilized surface (**Figure 5**). Self-thinning is usually related to competition, but we suggest

that in the riparian context another mechanism might take effect, namely altruism. If the aboveground parts of some trees die back, this will reduce the aerial density of the RSS stand. The crownless individuals will not produce seeds but might contribute to the reproduction of their grafted neighbours and decrease the aerial density of the stand (Tarroux and DesRochers, 2011). Indeed, as suggested by many studies undertaken in terrestrial contexts (Lev-Yadun, 2011), grafted trees that have lost their crown can leave a functional root system in the soil that is able to gather water and nutrients and store energy, which are then made available to the neighbouring connected trees. Here, the altruism shown by the trees may represent a (nonexclusive) alternative of self-induced thinning. This altruistic behaviour, however, can only evolve through kin selection and should thus mostly involve genetically related trees.
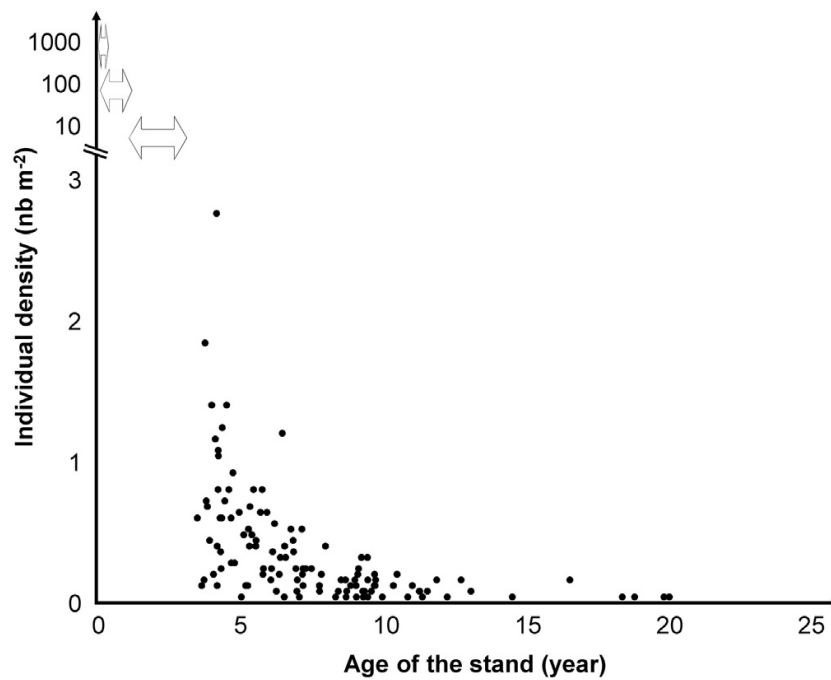

Figure 5. Relationship between stem density (i.e., number of stems of *Populus nigra* per square meter) and age of the stand on two wooded bars of the Garonne River, France. Stem density decreases as the age of the stand increases, moving from thousands of stems during the colonization phase to just a few stems in the mature phase (modified from Corenblit et al., 2016a).

8   Conclusions and future research

The conceptual framework of intraspecific interactions proposed in this article suggests that the process of fluvial landform construction and stabilisation within wooded riparian corridors could, at least partially, be related to positive intraspecific interactions among individuals of riparian *Salicaceae* species (i.e., intraspecific facilitation, cooperation, or altruism). We have described different mechanisms by which these positive intraspecific interactions may operate. We hope that this novel framework will stimulate further research at the interfaces between geomorphology, ecology, and evolutionary biology. This will help us understand the underlying biological mechanisms of biogeomorphic landform construction, stabilisation, and the ability to absorb disturbance before shifting into another state or stability domain, i.e., resilience. We suggest the following research topics for testing the nature and role of positive intraspecific interactions in fluvial landform and niche construction:

- The effect of RSS stand density and physiognomy on niche construction performance should be quantified. Dense stands composed of related individuals (kin) should have an enhanced capacity to trap fine sediment, organic matter, and nutrients and to reach sexual maturity between large destructive floods.

- The very fine scale genetic structure of RSS stands on biogeomorphic landforms (e.g., fluvial islands, benches, and floodplains) should be studied at different stages. Indeed, except for facilitation, positive intraspecific interactions can only be stable if they involve related individuals (kin selection). Interacting individuals in close proximity should therefore have a higher relatedness than the average in the population. Moreover, we expect these positive intraspecific interactions to specifically occur in dynamic river reaches. Thus, the fine scale genetic structure should vary in space and time along riparian corridors.

- Our knowledge about the importance and functioning of mycorrhizal communities within riparian woodlands should be deepened. In particular, we need to understand to what extent they participate in nutrient sharing among trees and, reciprocally, how much individual trees invest in their mycorrhizae. Here again, the relatedness of the trees should affect the maintenance of the mycorrhizal network.

- The direct exchange of nutrients between individuals through root grafts only needs to be clearly demonstrated and its functional mechanisms (e.g., does it involve raw or elaborated sap?) and consequences understood. We expect to find a more balanced exchange between related individuals (cooperation) than between unrelated individuals (parasitism).

- The self-thinning stage should be studied in more detail. In particular, we need to quantify the proportion of root systems that remain functional after crown dieback and study its effects on spatial and genetic stand structure and on nutrient acquisition capacities of tree groups. We expect crown dieback, implying tree mortality, to be an altruistic behaviour when related trees are interconnected through functional root grafts.

- The directed modification of the hydrogeomorphic environment may have repercussions on RSS evolution, possibly on the selection and fixation of engineer and nonengineer traits in the RSS population (such as cooperation and altruism traits). To study evolution, we need to compare settings with and without niche construction over several generations.

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References

Aberle, J., Järvelä, J., 2013. Flow resistance of emergent rigid and flexible floodplain vegetation. J. Hydraul. Res. 51 (1), 33–45.

Allen, M.F., 1991. The Ecology of Mycorrhizae. Cambridge University Press, Cambridge, UK.

Arens, P., Coops, H., Jansen, J., Vosman, B., 1998. Molecular genetic analysis of black poplar (Populus nigra L.) along Dutch rivers. Mol. Ecol. 7 (1), 11–18.

Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. Science 211 (27), 1390–1396.

Baldwin, I.T., Schultz, J.C., 1983. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. Science 221 (4607), 277–279.

Barsoum, N., Muller, E., Skot, L., 2004. Variations in levels of clonality among Populus nigra L. stands of different ages. Evol. Ecol. 18 (5–6), 601–624.

Bätz, N., Verrecchia, E.P., Lane, S.N., 2015. The role of soil in vegetated gravelly river braid plains: more than just a passive response? Earth Surf. Process. Landf. 40 (2), 143–156.

Beauchamp, V.B., Stromberg, J.C., Stutz, J.C., 2006. Arbuscular mycorrhizal fungi associated with Populus–Salix stands in a semiarid riparian ecosystem. New Phytol. 170 (2), 369–380.

Beddie, A.D., 1941. Natural root grafts in New Zealand trees. Transactions and Proceedings of the Royal Society of New Zealand. Vol. 76, pp. 199–203.

Bendix, J., Hupp, C.R., 2000. Hydrological and geomorphological impacts on riparian plant communities. Hydrol. Process. 14 (16–17), 2977–2990.

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9 (5), 191–193.

Bhatt, M.V., Khandelwal, A., Dudley, S.A., 2011. Kin recognition, not competitive interactions, predicts root allocation in young Cakile edentula seedling pairs. New Phytol. 189 (4), 1135–1142.

Biedrzycki, M.L., Bais, H.P., 2010. Kin recognition: another biological function for root secretions. Plant Signal. Behav. 5 (4), 401–402.

Biedrzycki, M.L., Jilany, T.A., Dudley, S.A., Bais, H.P., 2010. Root exudates mediate kin recognition in plants. Communicative & Integrative Biology 3 (1), 28–35.

Biedrzycki, M.L., Venkatachalam, L., Bais, H.P., 2011. Transcriptome analysis of Arabidopsis thaliana plants in response to kin and stranger recognition. Plant Signal. Behav. 6 (10), 1515–1524.

Bormann, F.H., Graham, B.F., 1959. The occurrence of natural root grafting in Eastern white pine, Pinus strobus L., and its ecological implications. Ecology 40 (4), 677–691.

Bornette, G., Tabacchi, E., Hupp, C., Puijalon, S., Rostan, J.C., 2008. A model of plant strategies in fluvial hydrosystems. Freshw. Biol. 53 (8), 1692–1705.

Bronstein, J.L., 1994. Our current understanding of mutualism. Q. Rev. Biol. 69 (1), 31–51.

Bronstein, J.L., 2009. The evolution of facilitation and mutualism. J. Ecol. 97 (6), 1160–1170.

Brooker, R.W., Callaghan, T.V., 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81 (1), 196–207.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. J. Ecol. 96 (1), 18–34.

Brownlee, C., Duddridge, J.A., Malibari, A., Read, D.J., 1983. The structure and function of mycelial systems of ectomycorrhizal roots with special reference to their role in forming inter-plant connections and providing pathways for assimilate and water transport. Plant Soil 71 (1), 433–443.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. Trends Ecol. Evol. 18 (3), 119–125.

Cahill Jr., J.F., McNickle, G.G., 2011. The behavioral ecology of nutrient foraging by plants. Annu. Rev. Ecol. Evol. Syst. 42 (1), 289–311.

Callaway, R.M., 2002. The detection of neighbors by plants. Trends Ecol. Evol. 17 (3), 104–105.

Chen, S.C., Chan, H.C., Li, Y.H., 2012a. Observations on flow and local scour around submerged flexible vegetation. Adv. Water Resour. 43, 28–37.

Chen, B.J.W., During, H.J., Anten, N.P.R., 2012b. Detect thy neighbor: identity recognition at the root level in plants. Plant Sci. 195, 157–167.

Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42 (4), 710–723.

Cooper, D.J., Merritt, D.M., Andersen, D.C., Chimner, M.A., 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the Upper Green River, USA. River Res. Appl. 15 (5), 419–440.

Corenblit, D., Steiger, J., Gurnell, A., Tabacchi, E., 2007a. Darwinian origin of landforms. Earth Surf. Process. Landf. 32 (13), 2070–2073.

Corenblit, D., Tabacchi, E., Steiger, J., Gurnell, A.M., 2007b. Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. Earth Sci. Rev. 84 (1–2), 56–86.

Corenblit, D., Steiger, J., Gurnell, A.M., Tabacchi, E., Roques, L., 2009. Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors. Earth Surf. Process. Landf. 34 (13), 1790–1810.

Corenblit, D., Steiger, J., González, E., Gurnell, A.M., Charrier, G., Darrozes, J., Dousseau, J., Julien, F., Lambs, L., Larrue, S., Roussel, E., Vautier, F., Voldoire, O., 2014. The biogeomorphological life cycle of poplars during the fluvial biogeomorphological succession: a special focus on Populus nigra L. Earth Surf. Process. Landf. 39 (4), 546–563.

Corenblit, D., Davies, N.S., Steiger, J., Gibling, M.R., Bornette, G., 2015. Considering river structure and stability in the light of evolution: feedbacks between riparian vegetation and hydrogeomorphology. Earth Surf. Process. Landf. 40 (2), 189–207.

Corenblit, D., Steiger, J., Charrier, G., Darrozes, J., Garófano-Gómez, V., Garreau, A., González, E., Gurnell, A.M., Hortobágyi, B., Julien, F., Lambs, L., Larrue, S., Otto, T., Roussel, E., Vautier, F., Voldoire, O., 2016a. Populus nigra L. establishment and fluvial landform construction: biogeomorphic dynamics within a channelized river. Earth Surf. Process. Landf. 41 (9), 1276–1292.

Corenblit, D., Vidal, V., Cabanis, M., Steiger, J., Garófano-Gómez, V., Garreau, A., Hortobágyi, B., Otto, T., Roussel, E., Voldoire, O., 2016b. Seed retention by pioneer trees enhances plant diversity resilience on gravel bars: observations from the river Allier, France. Adv. Water Resour. 93, 182–192.

Crain, C.M., Bertness, M.D., 2006. Ecosystem engineering across environmental gradients: implications for conservation and management. Bioscience 56 (3), 211–218.

Dawkins, R., 1976. The Selfish Gene. Oxford University Press, Oxford, UK.

Dawkins, R., 1982. The Extended Phenotype: the Long Reach of the Gene. Oxford University Press, UK.

Dawkins, R., 2004. Extended phenotype – but not too extended. A reply to Laland, Turner and Jablonka. Biol. Philos. 19 (3), 377–396.

Doty, S.L., Dosher, M.R., Singleton, G.L., Moore, A.L., van Aken, B., Stettler, R.F., Strand, S.E., Gordon, M.P., 2005. Identification of an endophytic Rhizobium in stems of Populus. Symbiosis 39 (1), 27–35.

Dudley, S.A., 2015. Plant cooperation. AoB Plants 7, plv113.

Dudley, S.A., File, A.L., 2007. Kin recognition in an annual plant. Biol. Lett. 3 (4), 435–438.

Dudley, S.A., Murphy, G.P., File, A.L., 2013. Kin recognition and competition in plants. Funct. Ecol. 27 (4), 898–906.

Eichel, J., Corenblit, D., Dikau, R., 2016. Conditions for feedbacks between geomorphic and vegetation dynamics on lateral moraine slopes: a biogeomorphic feedback window. Earth Surf. Process. Landf. 41 (3), 406–419.

Eriksson, O., Ehrlén, J., 2008. Seedling recruitment and population ecology. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.), Seedling Ecology and Evolution. Cambridge University Press, Cambridge, UK, pp. 239–254.

Erwin, D.H., 2008. Macroevolution of ecosystem engineering, niche construction and diversity. Trends Ecol. Evol. 23 (6), 304–310.

Euler, T., Zemke, J., Rodrigues, S., Herget, J., 2014. Influence of inclination and permeability of solitary woody riparian plants on local hydraulic and sedimentary processes. Hydrol. Process. 28 (3), 1358–1371.

Fajardo, A., McIntire, E.J.B., 2010. Merged trees in second-growth, fire origin forests in Patagonia, Chile: positive spatial association patterns and their ecological implications. Am. J. Bot. 97 (9), 1424–1430.

Fajardo, A., McIntire, E.J.B., 2011. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. J. Ecol. 99 (2), 642–650.

Fajardo, A., Torres-Díaz, C., Till-Bottraud, I., 2016. Disturbance and density-dependent processes (competition and facilitation) influence the fine-scale genetic structure of a tree species population. Ann. Bot. 117 (1), 67–77.

File, A.L., Klironomos, J., Maherali, H., Dudley, S.A., 2012a. Plant kin recognition enhances abundance of symbiotic microbial partner. PLoS One 7 (9), e45648.

File, A.L., Murphy, G.P., Dudley, S.A., 2012b. Fitness consequences of plants growing with siblings: reconciling kin selection, niche partitioning and competitive ability. Proc. R. Soc. Lond. B Biol. Sci. 279 (1727), 209–218.

Francis, R., Read, D.J., 1984. Direct transfer of carbon between plants connected by vesicular-arbuscular mycorrhizal mycelium. Nature 307 (5946), 53–56.

Francis, R.A., Corenblit, D., Edwards, P.J., 2009. Perspectives on biogeomorphology, ecosystem engineering and self-organisation in island-braided fluvial ecosystems. Aquat. Sci. 71 (3), 290–304.

Fraser, E.C., Lieffers, V.J., Landhäusser, S.M., 2005. Age, stand density, and tree size as factors in root and basal grafting of lodgepole pine. Can. J. Bot. 83 (8), 983–988.

Fraser, E.C., Lieffers, V.J., Landhäusser, S.M., 2006. Carbohydrate transfer through root grafts to support shaded trees. Tree Physiol. 26 (8), 1019–1023.

Gagliano, M., 2015. In a green frame of mind: perspectives on the behavioural ecology and cognitive nature of plants. AoB Plants 7, plu075.

Gardes, M., Bialet, E., Binet, E., Brousseau, C., Carré, F., Charcosset, J., Fradet, N., Griffith, P., Gryta, H., Laquerbe, M., 2003. Les symbiotes mycorhiziens du peuplier noir (Populus nigra L.): la spécificité des assemblages fongiques en milieu riverain. Les Actes du BRG 4, 453–466.

Gom, L.A., Rood, S.B., 1999a. Patterns of clonal occurrence in a mature cottonwood grove along the Oldman River, Alberta. Can. J. Bot. 77 (8), 1095–1105.

Gom, L.A., Rood, S.B., 1999b. The discrimination of cottonwood clones in a mature grove along the Oldman River in southern Alberta. Can. J. Bot. 77 (8), 1084–1094.

Gonneau, C., Jersáková, J., de Tredern, E., Till-Bottraud, I., Saarinen, K., Sauve, M., Roy, M., Hájek, T., Selosse, M.-A., 2014. Photosynthesis in perennial mixotrophic Epipactis spp. (Orchidaceae) contributes more to shoot and fruit biomass than to hypogeous survival. J. Ecol. 102 (5), 1183–1194.

Gorelick, R., Marler, T.E., 2014. Kin recognition by roots occurs in cycads and probably in conifers. Commun. Integr. Biol. 7 (1), e28009.

Graham, B.F., Bormann, F.H., 1966. Natural root grafts. Bot. Rev. 32 (3), 255–292.

Grime, J.P., Hodgson, J.G., Hunt, R., 2014. Comparative Plant Ecology: A Functional Approach to Common British Species. Springer, Netherlands (742 pp).

Gryta, H., Carriconde, F., Charcosset, J.-Y., Jargeat, P., Gardes, M., 2006. Population dynamics of the ectomycorrhizal fungal species Tricholoma populinum and Tricholoma scalpturatum associated with black poplar under differing environmental conditions. Environ. Microbiol. 8 (5), 773–786.

Gurnell, A., 2014. Plants as river system engineers. Earth Surf. Process. Landf. 39 (1), 4–25.

Gurnell, A., Tockner, K., Edwards, P., Petts, G., 2005. Effects of deposited wood on biocomplexity of river corridors. Front. Ecol. Environ. 3 (7), 377–382.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101 (1), 79–90.

Hamilton, W.D., 1963. The evolution of altruistic behavior. Am. Nat. 97 (896), 354–356.

Hamilton, W.D., 1964. The genetical evolution of social behaviour. I. J. Theor. Biol. 7 (1), 1–16.

Hardin, G., 1960. The competitive exclusion principle. Science 131 (3409), 1292–1297.

Harner, M.J., Opitz, N., Geluso, K., Tockner, K., Rillig, M.C., 2011. Arbuscular mycorrhizal fungi on developing islands within a dynamic river floodplain: an investigation across successional gradients and soil depth. Aquat. Sci. 73 (1), 35–42.

He, Q., Bertness, M.D., Altieri, A.H., 2013. Global shifts towards positive species interactions with increasing environmental stress. Ecol. Lett. 16 (5), 695–706.

Holloway, J.V., Rillig, M.C., Gurnell, A.M., 2017. Underground riparian wood: buried stem and coarse root structures of black poplar (Populus nigra L.). Geomorphology 279, 188–198.

Hortobágyi, B., Corenblit, D., Steiger, J., Peiry, J.-L., 2017. Niche construction within riparian corridors. Part I: exploring biogeomorphic feedback windows of three pioneer riparian species, Allier River, France. Geomorphology (in press).

Jelínková, H., Tremblay, F., DesRochers, A., 2009. Molecular and dendrochronological analysis of natural root grafting in Populus tremuloides (Salicaceae). Am. J. Bot. 96 (8), 1500–1505.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69 (3), 373–386.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78 (7), 1946–1957.

Karban, R., Yang, L.H., Edwards, K.F., 2014. Volatile communication between plants that affects herbivory: a meta-analysis. Ecol. Lett. 17 (1), 44–52.

Karrenberg, S., Edwards, P.J., Kollmann, J., 2002. The life-history of Salicaceae living in the active zone of floodplains. Freshw. Biol. 47 (4), 733–748.

Kirk, P.M., Cannon, P.F., David, J.C., Stalpers, J., 2001. Ainsworth and Bisby's Dictionary of the Fungi. 9th ed. CAB International, Wallingford, UK.

Laland, K.L., 2004. Extending the extended phenotype. Biol. Philos. 19 (3), 313–325.

Laland, K., Matthews, B., Feldman, M.W., 2016. An introduction to niche construction theory. Evol. Ecol. 30 (2), 191–202.

Lehmann, L., Keller, L., 2006. The evolution of cooperation and altruism– a general framework and a classification of models. J. Evol. Biol. 19 (5), 1365–1376.

Lepik, A., Abakumova, M., Zobel, K., Semchenko, M., 2012. Kin recognition is density dependent and uncommon among temperate grassland plants. Funct. Ecol. 26 (5), 1214–1220.

Lev-Yadun, S., 2011. Why should trees have natural root grafts? Tree Physiol. 31 (6), 575–578.

Lytle, D.A., Poff, N.L., 2004. Adaptation to natural flow regimes. Trends Ecol. Evol. 19 (2), 94–100.

Mahoney, J.M., Rood, S.B., 1998. Streamflow requirements for cottonwood seedling recruitment - an integrative model. Wetlands 18 (4), 634–645.

Mardhiah, U., Caruso, T., Gurnell, A., Rillig, M.C., 2016. Arbuscular mycorrhizal fungal hyphae reduce soil erosion by surface water flow in a greenhouse experiment. Appl. Soil Ecol. 99, 137–140.

Matthews, B., De Meester, L., Jones, C.G., Ibelings, B.W., Bouma, T.J., Nuutinen, V., van de Koppel, J., Odling-Smee, J., 2014. Under niche construction: an operational bridge between ecology, evolution and ecosystem science. Ecol. Monogr. 84 (2), 245–263.

McIntire, E.J.B., Fajardo, A., 2011. Facilitation within species: a possible origin of group selected superorganisms. Am. Nat. 178 (1), 88–97.

McIntire, E.J.B., Fajardo, A., 2014. Facilitation as a ubiquitous driver of biodiversity. New Phytol. 201 (2), 403–416.

Moulia, B., Coutand, C., Julien, J.-L., 2015. Mechanosensitive control of plant growth: bearing the load, sensing, transducing, and responding. Front. Plant Sci. 6 (52), 1–20.

Murphy, G.P., Dudley, S.A., 2009. Kin recognition: competition and cooperation in Impatiens (Balsaminaceae). Am. J. Bot. 96 (11), 1990–1996.

Odling-Smee, F.J., Laland, K.N., Feldman, M.W., 2003. Niche Construction: the Neglected Process in Evolution. Princeton University Press, Princeton, NJ, USA (472 pp).

Osakabe, Y., Yamaguchi-Shinozaki, K., Shinozaki, K., Tran, L.-S.P., 2013. Sensing the environment: key roles of membrane-localized kinases in plant perception and response to abiotic stress. J. Exp. Bot. 64 (2), 445–458.

Phillips, J.D., 2016. Landforms as extended composite phenotypes. Earth Surf. Process. Landf. 41 (1), 16–26.

Piotrowski, J.S., Lekberg, Y., Harner, M.J., Ramsey, P.W., Rillig, M.C., 2008. Dynamics of mycorrhizae during development of riparian forests along an unregulated river. Ecography 31 (2), 245–253.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime: a paradigm for river conservation and management. Bioscience 47 (11), 769–784.

Post, D.M., Palkovacs, E.P., 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. Philos. Trans. R. Soc. B 364 (1523), 1629–1640.

Righetti, M., 2008. Flow analysis in a channel with flexible vegetation using double averaging method. Acta Geophys. 56 (3), 801–823.

Rillig, M.C., Mummey, D.L., 2006. Mycorrhizas and soil structure. New Phytol. 171 (1), 41–53.

Rodrigues, S., Bréhéret, J.G., Macaire, J.J., Greulich, S., Villar, M., 2007. In-channel woody vegetation controls on sedimentary processes and the sedimentary record within alluvial environments: a modern example of an anabranch of the River Loire, France. Sedimentology 54 (1), 223–242.

Rood, S.B., Hillman, C., Sanche, T., Mahoney, J.M., 1994. Clonal reproduction of riparian cottonwoods in southern Alberta. Can. J. Bot. 72 (12), 1766–1774.

Rood, S.B., Patiño, S., Coombs, K., Tyree, M.T., 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. Trees-structure and function 14 (5), 248–257.

Rykiel, E.J., 1985. Towards a definition of ecological disturbance. Aust. J. Ecol. 10 (3), 361–365.

Sahney, S., Benton, M.J., Ferry, P.A., 2010. Links between global taxonomic diversity, ecological diversity and the expansion of vertebrates on land. Biol. Lett. 6 (4), 1–4. Scott, M.L., Shafroth, P.B., Auble, G.T., 1999. Responses of riparian cottonwoods to alluvial water table declines. Environ. Manag. 23 (3), 347–358.

Scott, M.L., Lines, G.C., Auble, G.T., 2000. Channel incision and patterns of cottonwood stress and mortality along the Mojave River, California. J. Arid Environ. 44 (4), 399–414.

Scott-Phillips, T.C., Laland, K.N., Shuker, D.M., Dickins, T.E., West, S.A., 2014. The niche construction perspective: a critical appraisal. Evolution 68 (5), 1231–1243.

Semchenko, M., Saar, S., Lepik, A., 2014. Plant root exudates mediate neighbour recognition and trigger complex behavioural changes. New Phytol. 204 (3), 631–637.

Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M., Molina, R., 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388 (6642), 579–582.

Stallins, J.A., 2006. Geomorphology and ecology: unifying themes for complex systems in biogeomorphology. Geomorphology 77 (3–4), 207–216.

Stallins, J.A., Corenblit, D., 2017. Accepted. Barrier dune biogeomorphic resilience in a geographic context. Geomorphology (this press).

Stromberg, J.C., Fry, J., Patten, D.T., 1997. Marsh development after large floods in an alluvial, arid-land river. Wetlands 17 (2), 292–300.

Tabacchi, E., Lambs, L., Guilloy, E., Planty-Tabacchi, A.M., Muller, E., Décamps, H., 2000. Impacts of riparian vegetation on hydrological processes. Hydrol. Process. 14 (16–17), 2959–2976.

Tarroux, E., DesRochers, A., 2010. Frequency of root grafting in naturally and artificially regenerated stands of Pinus banksiana: influence of site characteristics. Can. J. For. Res. 40 (5), 861–871.

Tarroux, E., DesRochers, A., 2011. Effect of natural root grafting on growth response of jack pine (Pinus banksiana; Pinaceae). Am. J. Bot. 98 (6), 967–974.

Tarroux, E., DesRochers, A., Krause, C., 2010. Effect of natural root grafting on growth response of jack pine (Pinus banksiana) after commercial thinning. For. Ecol. Manag. 260 (4), 526–535.

Tarroux, E., DesRochers, A., Tremblay, F., 2014. Molecular analysis of natural root grafting in jack pine (Pinus banksiana) trees: how does genetic proximity influence anastomosis occurrence? Tree Genet. Genomes 10 (3), 667–677.

Till-Bottraud, I., Fajardo, A., Rioux, D., 2012. Multi-stemmed trees of Nothofagus pumilio second-growth forest in Patagonia are formed by highly related individuals. Ann. Bot. 110, 905–913.

Vandenbussche, F., Pierik, R., Millenaar, F.F., Voesenek, L.A.C.J., Van Der Straeten, D., 2005. Reaching out of the shade. Curr. Opin. Plant Biol. 8 (5), 462–468.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37 (1), 130–137.