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Short review

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ENVIRONMENTAL HETEROGENEITY CONTROLS ORGANIC-MATTER DYNAMICS IN RIVER-FLOODPLAIN ECOSYSTEMS

ABSTRACT: Environmental heterogeneity is a key regulator of ecological processes. Riverine floodplains are particularly heterogeneous and dynamic systems and loss of their natural environmental heterogeneity and dynamism as a consequence of human impacts constitutes their most serious threat. On river floodplains, flow and flood pulses create a shifting mosaic of channels, ponds, bars, islands, and riparian forest patches. Composition and spatial arrangement of these habitat patches determine their degree of connectivity, which in turn controls the flux of matter and energy among adjacent patches. In light of these attributes, riverine floodplains are model ecosystems for studying the effect of heterogeneity on ecological processes. In this article we introduce a conceptual model for river-floodplain ecosystems that unifies leaf decomposition, organic-matter input, storage and quality, and stresses the importance of the flow and inundation regime. In combining these aspects of organic matter dynamics, which have been treated separately in the ecological literature, this model fosters a more holistic perspective of ecosystem processes on riverine floodplains. We conclude that the linkage between natural heterogeneity and ecosystem processes needs to be considered in future river-floodplain restoration projects.

KEY WORDS: leaf breakdown, decomposition, ecosystem process, flow regime, biodiversity, Tagliamento River, braided river

1. ENVIRONMENTAL HETEROGENEITY AND THE SHIFTING HABITAT MOSAIC

Environmental heterogeneity is defined as variance in patterns and processes over space and time (Kolasa and Rolle 1991). Physical complexity of an ecosystem, i.e. composition and configuration of habitats, is the key component of heterogeneity and one that mediates ecosystem functioning (Cardinale *et al.* 2002).

Natural riverine floodplains are among the most diverse and dynamic of all Earth's ecosystems (Tockner and Stanford 2002, Tiegs and Pohl 2005). Riverine floodplains consist of a shifting mosaic of aquatic, semi-aquatic and terrestrial landscape elements. While these elements change their location, size and configuration over time, the overall abundance of various elements often remains constant, a phenomenon referred to as "the shifting habitat mosaic" (Arscott *et al.* 2002, Stanford *et al.* 2005). If such a habitat mosaic consists of elements which exchange mass, energy, organisms, or information with one another, as it is the case for riverine floodplain habitats, they can be referred to as interactive (Lovett *et al.* 2005).

Here, we introduce a conceptual model of how environmental heterogeneity controls coarse-particulate organic-matter dynamics. Our model stems from ongoing research of the braided Tagliamento River in northeastern Italy (46°00'N, 12°30'E). The Tagliamento is among the last large reference rivers in Europe and offers a rare opportunity to study patterns and processes across different scales under near-natural conditions (Tockner *et al.* 2003).

2. ORGANIC MATTER AND DECOMPOSITION DYNAMICS ARE HETEROGENEOUS

In functioning as a vital source of carbon and energy to streams and rivers, allochthonous organic matter links terrestrial with aquatic ecosystems, and decomposition of this matter is a key ecosystem-level process (Webster and Benfield 1986, Langhans and Tockner 2006). Organic matter accumulates and is temporarily stored in depositional areas where it is pre-processed prior to its further transfer to other habitats (Mayack *et al.* 1989, Merritt and Lawson 1992). Particularly during floods, exchange of organic matter between the river and its adjacent riparian zone can be widespread (Neatrou *et al.* 2004). Decomposition of leaf litter has been widely investigated in both aquatic and terrestrial environments (Boulton and Boon 1991, Gessner *et al.* 1999), but few studies have addressed decomposition of leaf litter across heterogeneous environments such as river-floodplain ecosystems (Chergui and Pattee 1990, McArthur *et al.* 1994, Baldy *et al.* 2002). Physico-chemical conditions, composition and abundance of the decomposer community, leaf-litter quality (Gessner and Chauvet 1994), and the flow regime differ across these environments and control decomposition processes (Langhans and Tockner 2006). Rapid decomposition can occur under permanent inundation (Herbst and Reice 1982) as well as under highly fluctuating water levels (Battle and Golladay 2001). By separating the effects of duration and frequency of inundation, Langhans and Tockner (2006) found that duration of inundation is the main inundation component that con-

trols leaf decomposition in gravel bed rivers. Additionally, leaf decomposition was found to be faster in channels than in ponds in a floodplain reach of the Tagliamento River (S.D. Langhans - unpublished), and faster in humid than in dry riparian habitats (Hutchens and Wallace 2002).

In order to understand organic-matter dynamics in complex river-floodplain ecosystems, aspects of aquatic and terrestrial leaf decomposition need to be linked with input, storage and quality of organic matter, as well as with the character of the flow regime. The conceptual model we present here unifies components of organic-matter dynamics and illustrates how these components, which have been treated separately in the ecological literature, interact on riverine floodplains.

3. ORGANIC-MATTER DYNAMICS: A CONCEPTUAL MODEL FOR RIVER-FLOODPLAIN ECOSYSTEMS

Unconstrained river-floodplain ecosystems, such as the Tagliamento River, are characterized by a heterogeneous mosaic of channels, parafluvial and orthofluvial ponds, exposed gravel, vegetated islands and riparian forest (Fig. 1). Composition and spatial arrangement of these habitats determine the interface character among adjacent habitats, which in turn controls the flux of energy and matter through the ecosystem (Naiman and Décamps 1997). In contrast to terrestrial habitats, the length of aquatic-terrestrial interfaces, which determines the interaction potential among adjacent habitats, varies with river stage. The connectivity among and within river-floodplain habitats is controlled by fluvial dynamics which are driven by the flow regime and morphology of the floodplain (Fig. 1 A). In regulated compared to natural river systems for example, frequency and duration of inundation often decrease and the exchange of material becomes less frequent and more pulsed.

Riparian forests and vegetated islands are highly productive (Naiman and Décamps 1997) and contribute resources to less-productive aquatic and terrestrial habitats. Spatial arrangement of individual habitat patches governs input and distribution of leaf litter across the floodplain. For example, aerial

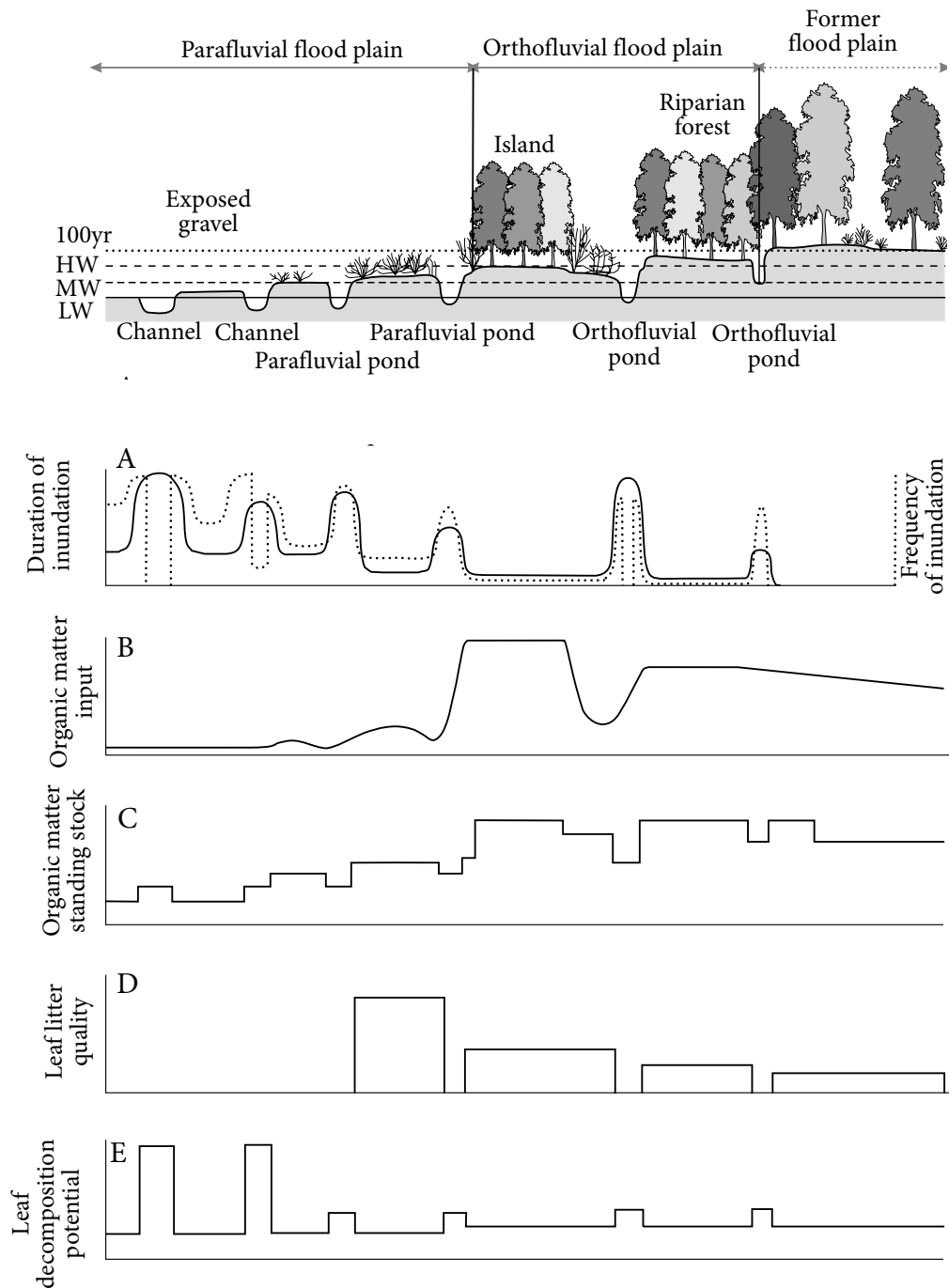


Fig. 1. A conceptual model for braided river-floodplains based on observations from the Tagliamento River (NE-Italy). Characterization of aquatic and terrestrial habitats across a river-upland transect: Components of the natural flow regime include duration (% of time) and frequency (number of events) of inundation (A). Input (g dry mass m⁻²; B) and distribution heterogeneity (g dry mass m⁻²; C) of particulate organic matter. Leaf-litter quality of donor trees (D). Leaf decomposition potential ($k = \text{decomposition coefficient (d}^{-1}\text{)}$; E). LW, MW, HW = low, mean and high water level; 100 year = flood event with a 100 years recurrent interval.

and lateral litter input declines exponentially with distance from their source (Fig. 1 B, Zah and Uehlinger 2001), and varies with wind speed and direction, and slope of the terrain. Due to the heterogeneous nature of river-floodplain ecosystems, the same habitat type, for example parafluvial ponds, can display highly different input-characteristics depending on its position relative to other habitats. Organic matter standing stock (Fig. 1 C) integrates input (transport across boundaries), retention and decomposition. Physical retention depends on relief and vegetation cover, as well as on large wood and channel roughness (Bilby and Likens 1980, Gurtz *et al.* 1988). Losses include decomposition and flood-related export. A major component of deposited coarse particulate organic matter is leaves (van der Nat 2002), which in temperate zones enter the system during abscission in autumn. Leaf-litter quality is highly variable across a floodplain transect and often decreases from the active zone towards the riparian forest (Fig. 1 D) because of the subsequent increasing proportion of hardwood tree species (Ostrowsky 1997). This gradient of leaf-litter quality is related to the successional stage of the vegetation, which in turn is determined by the disturbance regime. The decomposition of leaf litter is strongly affected by its quality (Naiman *et al.* 2005). For example, lignin content of leaf litter was found to be the best predictor for decomposition in aquatic and terrestrial systems (Gallardo and Merino 1993, Gessner and Chauvet 1994). Therefore, floodplain habitats supplied with higher quality leaves (i.e. lower lignin content) experience faster decomposition rates than habitats with input of low quality leaves. However, leaf decomposition potential (i.e. the maximal capacity of a habitat to decompose leaves not limited by environmental factors) in floodplain habitats is highest in channels (i.e. highest decomposition coefficient k), medium in ponds, and lowest in terrestrial habitats (S.D. Langhans - unpublished, Fig. 1 E).

In natural river-floodplain ecosystems, the area of aquatic habitats relative to other floodplain habitats can be small and these less abundant habitats have a significantly higher decomposition potential than highly abun-

dant terrestrial habitats (i.e. exposed gravel, riparian forest). Interestingly, despite having the highest decomposition potential, aquatic habitats have low organic-matter input and standing stock. Large areas with relatively low decomposition potential often have high organic-matter input and standing stock (e.g. vegetated islands and riparian forest patches, Fig. 1). This mismatch effect is reduced when floods mix and redistribute organic matter and deposit it during falling water level. Pre-processed organic matter with a more homogenous quality is now more evenly distributed among floodplain habitats. Therefore, at local scales flood pulses control leaf decomposition via the flow regime and more broadly by linking sources of organic matter with areas of high decomposition potential.

4. IMPLICATIONS

Worldwide, the loss of heterogeneity, largely through alteration of the flow regime and channelization, is the most serious threat to the ecological integrity of riverine floodplains (Dobson *et al.* 1997, Bunn and Arthington 2002). Flow regulation reduces flood intensity, duration and frequency (McMahon and Finlayson 2003). Regulated systems mostly lack channel-forming flows and intense water flux through the alluvial aquifer leading to a loss in dynamics and heterogeneity of the shifting habitat mosaic (Stanford *et al.* 2005). Parafluvial and orthofluvial ponds, alluvial channels and vegetated islands disappear and habitat diversity decreases. Lateral connectivity among floodplain habitats is severed, and flow and flood pulses no longer function as reorganizers of organic matter which can lead to drastic changes on the ecosystem process level. Additionally, channelization results in a loss of areas with low decomposition potential, such as gravel bars, and in an increase in the relative proportion of high decomposition potential areas, such as channels. As a result, the decomposition process and the transport of organic matter are altered with potential consequences for higher trophic levels in downstream ecosystems. An additional effect of flow regulation and channelization is that the input of leaves into active floodplain habitats decreases, whereas storage of leaf

litter in vegetated zones (e.g. riparian forest, islands) increases. As a result, diversity within the litter layer decreases, which can negatively affect litter turnover rates (Hoorens *et al.* 2003).

It is crucial to quantify effects of environmental heterogeneity on ecosystem-level processes to understand the links between heterogeneity and the functioning of river-floodplain ecosystems. Knowledge of natural variance in such environments should be integrated in future restoration approaches, which so far are often site specific and therefore do not consider the heterogeneous character of riverine systems. Our model promotes a holistic perspective including interactions among habitats in a mosaic shaped environment. In the future, heterogeneity needs to be seen as an inherent part in river restoration projects.

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