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Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats

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ABSTRACT

Floodplains have been strongly altered by human activities such as channelization and other river regulations. Globally, there is a growing interest in their restoration because of an increasing understanding of the ecological importance of these habitats for feeding, spawning, nursery or overwintering of aquatic species. In this study, a large floodplain restoration project of the upper Danube River was used to investigate colonization and succession patterns of fish, macroinvertebrates, macrophytes and periphyton in relation to abiotic habitat variables that can be restored through ecosystem management. Highest species diversity was detected near the contact zones of the floodplain channel to the main stem of the Danube, and in the transition zones of river sections (RS) and oxbow lakes (OS). The highest proportions of all taxa (82%) and of distinctive species (22%) were detected in RS, followed by OS (66% of all taxa, 8% distinctive species) and floodplain ponds (FP, 47% of all taxa, 5% distinctive species). The habitat types RS, OS and FP significantly differed in overall community composition and their colonization processes comprising fast colonization of current-adapted specialists in RS, and mostly generalist species in OS and FP. Our results indicate that restoration of floodplain habitats should not only consider the re-establishment of maximum connectivity, but also provide a mosaic of distinct habitat types with different degrees of connectivity and disturbance. Each habitat type in the floodplain supported a unique assemblage of species, which suggests that such habitat mosaics can facilitate exceptionally diverse ecosystems.

1. Introduction

River floodplains are disturbance-dependent ecosystems, providing a complex mosaic of freshwater habitats that are characterized by their spatio-temporal heterogeneity and a gradient in hydrological connectivity with the main channel (Junk et al., 1989; Ward and Stanford, 1995a, 1995b; Ward et al., 1999). Permanent and temporary aquatic habitats within river floodplains are of high importance for species richness and productivity in riverine landscapes (Tockner and Stanford, 2002; Ward and Tockner, 2001), providing habitats for feeding, spawning, nursery or overwintering for many fluvial species (Cucherousset et al., 2008; Williams, 2006; Molls, 1999; Cunjak, 1996; Ward and Stanford, 1995a). They are considered biodiversity hotspots, as their diversity is often higher than in the fringing landscape (De Jager et al., 2012; Knutson and Klaas, 1998; Malanson, 1993). However, large river floodplain ecosystems have been strongly altered by anthropogenic activities and have often diminished due to river regulations such as river straightening, bank stabilization, creation of impoundments, and hydropower use (Ward et al., 1999). These alterations interrupt the longitudinal connectivity in river systems (Dynesius and Nilsson, 1994; Mueller et al., 2011) and cause a suppression of the natural disturbance regime, disrupting the lateral connectivity between floodplain habitats and the main river as well. This disruption of longitudinal and lateral connectivity can severely disturb the flood pulse (Junk et al., 1989), restrict dynamic processes of high and low water levels and different degrees of sediment and deadwood dynamics, which are responsible for the continuous creation of new aquatic habitats in the floodplain (Hohensinner et al., 2004). An interruption of the flood pulse and restricted connectivity lead to an aging of aquatic habitats. Especially in floodplain ponds and oxbow lakes, this results in similar community compositions and reduced species numbers due to reaching a terminal state of succession. Early successional stages of such stagnant waterbodies in the floodplain provide important habitats, particularly to macrophytes, as well as to specifically adapted fish (Grift et al., 2006) and macroinvertebrates (Reckendorfer et al., 2006). Additionally, impoundments can severely affect timing and intensity of channel-forming processes of floodplain rivers, interrupting species migration (fish: Grift, 2001; Burgess et al., 2013; macroinvertebrates: Paillex et al., 2009; macrophytes: Geest et al., 2005; fish and macroinvertebrates, macrophytes and plankton: Admiraal et al., 1993),

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sediment transport (Nilsson and Berggren, 2000), lead to alterations of natural groundwater levels (Stammel et al., 2012; Stammel et al., 2016) and in consequence to a strong change of the floodplain plant community (Alexander et al., 2008; Ward and Stanford, 1995b).

As a logical consequence, severe changes in floodplain community composition, successional stages and associated declines in species richness have been recorded by several authors and in different regions (Dister et al., 1990; Ward and Stanford, 1995a; Bayley, 1995).

Recently, there is a globally growing interest in restoring river floodplains and river-floodplain connectivity (e.g. Europe: Danube, Hein et al., 2016; Habersack et al., 2016; Rhine, Grift, 2001; North America: Mississippi, De Jager et al., 2012; Kissimmee, Dahm et al., 1995; Australia: Murray-Darling, MacNally et al., 2002; Asia: Mekong, Albers and Schmitt, 2015; Banshi, Mamun, 2010) because of an increased understanding of the ecological importance of floodplain habitats for river ecosystems (Feyrer et al., 2006). Furthermore, there is an increasing number of legal requirements such as the European Water Framework Directive (European Parliament, 2000) or the North American Clean Water Act (92nd United States Congress, 1972).

Due to the complexity of floodplain restoration, the restoration of connectivity, water level dynamics and habitats such as oxbow lakes, floodplain rivers and floodplain ponds needs to be evidence-based (Pander and Geist, 2013; Geist, 2015; Geist and Hawkins, 2016). Whilst these principles are well considered in other habitat types, such as the restoration of instream variables in rivers (e.g. spawning grounds for salmonids: Mueller et al., 2014a; deadwood introductions: Pander and Geist, 2016; restoring bank habitats for juvenile fishes: Pander et al., 2017), critical analyses on the effects of floodplain restoration that simultaneously consider different taxonomic groups (fish, macroinvertebrates, macrophytes and periphyton) are rare (Admiraal et al., 1993, for plankton, macrophytes, invertebrates, and fish from published literature data) and studies considering different taxonomic groups sampled simultaneously in the same habitats are absent. Thus, scientifically founded management implications for successful restoration of these specific floodplain habitats cannot be drawn yet.

In this study, fish, macroinvertebrate, macrophyte, and periphyton communities were sampled over a four-year period simultaneously in the habitat types floodplain rivers, oxbow lakes and floodplain ponds within a major floodplain restoration project at the upper Danube River (Stammel et al., 2012). This dataset was investigated for seasonal patterns of colonization and succession to assess which measures constitute the most desired effects on aquatic communities to make future floodplain restoration effective and successful.

The main objective of this study was to identify how connectivity to the Danube and the transition zones between habitats affect spatial biodiversity patterns and colonization as well as which habitat types harbour greatest biodiversity across the taxonomic groups of fish, macroinvertebrates, macrophytes and periphyton.

In particular, we hypothesized that colonization and succession patterns of the restored floodplain habitats are determined by (i) habitat type (rivers, oxbow lakes and floodplain ponds), (ii) taxonomic group and associated distinctive species traits such as current preference, and (iii) connectivity as well as distance to the main channel Danube. We also hypothesized that (iv) overall biodiversity is more strongly dependent on the provision of a mosaic of different habitat types or their transition zones between the habitats, or the connection to the main source Danube rather than on the provision of one specific type of habitat within the restoration.

2. Material and methods

2.1. Study area

The study was carried out at the Danube River in Germany between the cities Neuburg and Ingolstadt (Stammel et al., 2012; Pander et al., 2015; Pander et al., 2016). The study area is located within the largest remaining contiguous alluvial forest and extends over 12 km^2 in direct proximity to the power plant Bergheim (km 2470; 48°45′00.74″N, 11°15′57.79″E to km 2459; 48° 44′13.58″N, 11°19′54.07″E). The discharge at this part of the upper Danube (mean annual discharge = 313 $m^3 s^{-1}$) is highly influenced by two major alpine rivers: the Iller and the Lech, which both are characterized by snow-melt induced summer peak flows. Like many major European rivers, the Danube was subject to substantial changes to its hydraulics and sediment regime over centuries. Main drivers of degradation were flood protection, hydropower use and land reclamation resulting in channel straightening, embankment, reduced sediment transport, interruption of the river continuum, and disconnection from the floodplain. Today the Danube is impounded by 78 major barriers, with increasing density towards the upstream areas (Habersack et al., 2016).

2.2. Floodplain restoration

To revert the negative effects on aquatic and terrestrial habitats and biodiversity, a new floodplain river (NFR) was constructed and first flooded in June 2010 in the context of a large restoration project led by the local water authorities of Ingolstadt, Germany. The major goal of the restoration was to restore the last remaining ancient alluvial forest of the Danube River in Germany. The new river section was intended to reconnect the Danube with its former floodplain, to increase groundwater levels, provide additional freshwater habitat and restore the river continuum by bypassing the hydropower plant Bergheim (Fig. 1). The discharge of the NFR ranges between 1.5 $m^3 s^{-1}$ and 5 $m^3 s^{-1}$ and is dynamically regulated corresponding to the discharge of the Danube (Fig. 2), with a maximum discharge of 5 $m^3 s^{-1}$ during enhanced flow conditions in the Danube of up to 600 $m^3 s^{-1}$ and 1.5 $m^3 s^{-1}$ during low flow conditions in the Danube (< 150 $m^3 s^{-1}$). Moreover, the area can be flooded artificially through an additional inlet (ecological flooding) with a maximum of 25 $m^3 s^{-1}$ during high flow conditions of the Danube (discharge Danube > 600 $m^3 s^{-1}$, measured at the water gauge Neuburg 48°44′17.49″N, 11°10′49.71″, Stammel et al., 2012). The NFR has a total length of 9 km and was built following a nature-oriented construction scheme with structural enrichment such as boulders and dead wood. In some sections, gravel was introduced. Besides newly built river sections, the NFR consists of formerly temporary or very small Danube tributaries, which are now permanently flowing (e.g. Zeller Kanal) and former disconnected oxbow lakes of different successional stages as described in Stammel et al. (2012). This habitat type comprised shallow and deep oxbow lakes, of which some were formerly completely disconnected from the Danube or only connected during major flood events (every 10 to 15 years). After the reconnection, these OS became low flowing habitats dominated by reeds and pond-lilies. In close proximity to the NFR, there are several permanent small floodplain ponds which were formerly only connected to the Danube under extreme flow conditions (every 10 to 15 years). These ponds also contribute to aquatic biodiversity since some of them are now connected to the new floodplain river during high flow conditions (e.g. ecological flooding, Pander et al., 2015, Figs. 1 and 3). All river sections of the NFR are further referred to as RS, the oxbow lakes to OS and the floodplain ponds to FP. RS at the direct connection to OS are further referred to as transition zones, but not treated as a separate habitat type due to their RS-typical morphology (Fig. 3).

2.3. Study design

To study the effects of the floodplain restoration on aquatic biodiversity, all occurring aquatic habitat types RS, OS and FP (Fig. 3) were seasonally assessed in spring and summer. The aquatic biodiversity assessment was carried out in April 2010 before the opening of the NFR and seasonally after the opening of the NFR in August 2010, April 2011, August 2011, April 2012, August 2012, April 2013 and August 2013. A total of 37 sampling stretches (each comprising 30 m) including 15