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Wartime scars or reservoirs of biodiversity? The value of bomb crater ponds in aquatic conservation

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ABSTRACT

Considering the ongoing loss of aquatic habitats, anthropogenic ponds are gaining importance as substitute habitats. It is therefore important to assess their functioning in comparison to their natural precursors. Here we assess the biodiversity value of sodic bomb crater ponds by comparing their gamma diversity to that of natural reference habitats, astatic soda pans, and assess their importance on the landscape level by studying alpha and beta diversity. We studied aquatic organisms ranging from algae to vertebrates in a dense cluster of 54 sodic bomb crater ponds in Central Europe. Despite the overall small area of the pond cluster, gamma diversity was comparable to that found in surveys of natural habitats that encompassed much wider spatial and temporal scales. We also found a considerable number of species shared with reference habitats, indicating that these anthropogenic habitats function as important refuge sites for several species that are associated with the endangered soda pans. Moreover, we found a number of regionally or worldwide rare species. Among the components of beta diversity, species replacement dominated community assembly. Individual ponds contributed similarly to beta diversity in terms of replacement, being equally important for maintaining high gamma diversity and emphasising the role of the pond network rather than individual ponds. This pattern was seen in all studied groups. Bomb crater ponds therefore acted as important contributors to aquatic biodiversity. Considering the tremendous losses of ponds throughout Europe, anthropogenic ponds should be taken into consideration in nature conservation, especially when occurring in pond networks.

1. Introduction

Ponds are the most numerous representatives of inland standing waters (Downing et al., 2006). They host unique flora and fauna and contribute over-proportionally to regional biodiversity (De Meester et al., 2005; Oertli et al., 2005) and global biogeochemical cycles (Downing et al., 2008; Downing, 2010). Currently, there is a growing interest in pond ecology within community ecology and conservation biology (De Meester et al., 2005; Oertli et al., 2009), mostly due to the recent revelation and acknowledgement of their general ecological importance (Céréghino et al., 2014). Small waterbodies are especially vulnerable to climate change and habitat degradation (including pollution, fish stocking) due to their limited volume (Biggs et al., 2005; Brooks, 2009). The estimated loss of ponds in the 20th century exceeds 50% in many European countries, and it is even up to 90% in some regions mainly related to agricultural land drainage and urbanisation (Hassall, 2014; Wood et al., 2003). Recognising the drastic loss of ponds, restoration and reconstruction projects were recently implemented in several regions worldwide (Frisch and Green, 2007; Shulse et al., 2010; Williams et al., 2010). Ponds created for human purposes or as a side effect of various anthropogenic activities are widespread, and may act as important surrogate habitats for species of which the natural habitats have been lost. However, we generally lack information how anthropogenic freshwater habitats, including ponds, support biodiversity (Chester and Robson, 2013).

Conservation actions usually aim at maximising diversity either at the local (alpha) or at the landscape level (gamma diversity). Naturally,

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these two entities are inherently linked through community turnover among habitats (beta diversity), but beta diversity itself is rarely considered explicitly (Airoldi et al., 2008; McKnight et al., 2007; Socolar et al., 2016). Directly addressing beta diversity involves the analysis of spatial heterogeneity in addition to the link between local environment and community composition, hence such an approach helps identifying factors and processes maintaining diversity on the landscape level (Fairbanks et al., 2001; Margules and Pressey, 2000; McKnight et al., 2007). Detailed analyses of community turnover in space are predominantly done in terrestrial systems (although examples for aquatic systems also exist, e.g. Al-Shami et al., 2013; Maloufi et al., 2016). In context of the ongoing loss of aquatic habitats, the role of spatial heterogeneity and the explicit analysis of beta diversity represent a particular gap (Socolar et al., 2016). Beta diversity of small aquatic habitats such as ponds is generally considered to be high, serving as a frequent argument for the importance of their conservation (De Meester et al., 2005), but this is rarely taken into consideration in their practical conservation which relies on prioritizing individual habitats (Hill et al., 2016).

Different organism groups may display various levels of congruence in their regional distribution patterns. Their simultaneous consideration enables us to achieve a more holistic understanding on the assembly of communities and more efficient conservation planning (Paavola et al., 2003; Schouten et al., 2010). However, when it comes to ponds, most studies have surveyed them as habitats for amphibians (e.g. Beja and Alcazar, 2003; Knutson et al., 2004; Ruhí et al., 2012), macroinvertebrates (e.g. Becerra-Jurado et al., 2012; Céréghino et al., 2008; Wood et al., 2001) or plankton (e.g. De Bie et al., 2007; Gallego et al., 2012; Mimouni et al., 2015), while biodiversity studies simultaneously considering different organism groups are much rarer (exceptions include e.g. De Bie et al., 2012; De Marco et al., 2013; Lemmens et al., 2013).

We aim here to assess the biodiversity value of a peculiar type of anthropogenic habitat, bomb crater ponds. These habitats occur all over the world in areas affected by military activities in the past 100 years. In our study region, the Pannonian Plain in Central Europe, they form very dense clusters of habitat patches. They were created mainly by military exercises over the last 70 years or mistargeted bombings during World War II. Being considered wartime scars, many of these bomb crater ponds are currently subject to grassland rehabilitation measures (including filling most of them in). These measures are typically applied without a proper evaluation of their contemporary biodiversity. Due to their common origin, bomb crater ponds represent morphologically very similar habitats. Additionally, ponds within clusters were created at the same time and in restricted geographic regions, providing ideal model systems to study how anthropogenic ponds maintain biodiversity on a spatial scale where most conservation efforts take place. In general, we know very little about their aquatic communities, and so far they have never been specifically addressed by regional-scale studies.

As a model system, we chose a confined area harbouring a dense cluster of bomb craters situated in Central Hungary (54 ponds within a 1 km scale). We sampled these habitats simultaneously for benthic diatoms, zooplankton, macroinvertebrates and amphibians. Our first aim is to quantify their entire species inventory at the landscape level (gamma diversity) and compare it to other natural habitats in the region. Second, we aim to investigate how the observed gamma diversity is maintained within the cluster of bomb crater ponds by studying alpha and beta diversity (along with its components), and identify their main environmental drivers. More specifically, we test whether the individual contribution of ponds to the total variation (i.e. beta diversity) is similar or some habitats are unique biodiversity hotspots and should have higher conservation priority. By targeting multiple organism groups, we will also investigate whether there is a congruence pattern in diversity among them.

2. Materials and methods

2.1. Study area

The Pannonian Plain in Central Europe is characterised by diverse aquatic habitats, including a variety of ponds and pools (Boven et al., 2008a; Lukács et al., 2013), and even regionally restricted unique habitats with high conservation value such as the astatic soda pans, which are inland saline waters (Boros et al., 2014; Horváth et al., 2013a). The Kiskunság region in Hungary is a central part of the Plain, located on the interfluve of two large rivers, Danube and Tisza. It encompasses a diverse array of both aquatic (shallow lakes, swamps, peat bogs, sodic marshes, soda pans, temporary pools etc.) and terrestrial habitats (wet and dry meadows, sandy and sodic grasslands, semi-arid sand dunes, steppes etc.). These altogether allow the existence of a unique flora and fauna, with a high number of rare and endemic species (Boven et al., 2008b; Kovács-Láng et al., 2008; Ladányi et al., 2015). Large parts of the region belong to the Kiskunság National Park and are parts of a

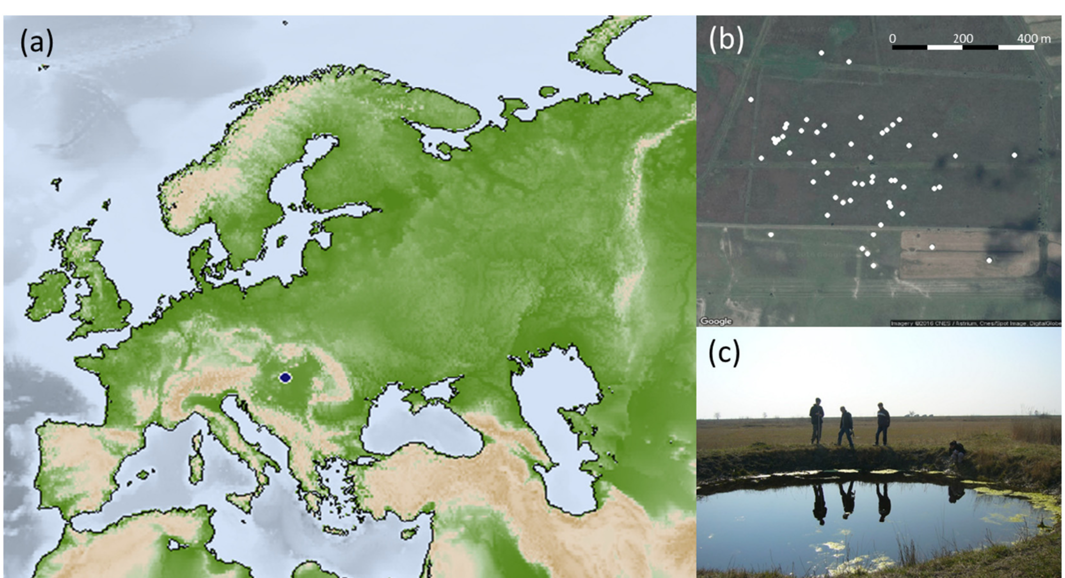

Fig. 1. The location of the study area in Europe (a) along with a map (b) and one example (c) of the habitats. On panel (b), the 54 ponds sampled within the study are indicated with filled white circles.