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Buried alive: Aquatic plants survive in 'ghost ponds' under agricultural fields

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ABSTRACT

The widespread loss of wetlands due to agricultural intensification has been highlighted as a major threat to aquatic biodiversity. However, all is not lost as we reveal that the propagules of some aquatic species could survive burial under agricultural fields in the sediments of 'ghost ponds' - ponds in-filled during agricultural land consolidation. Our experiments showed at least eight aquatic macrophyte species to germinate from seeds and oospores, following 50–150 years of dormancy in the sediments of ghost ponds. This represents a significant proportion of the expected macrophyte diversity for local farmland ponds, which typically support between 6 and 14 macrophyte species. The rapid (< 6 months) re-colonisation of resurrected ghost ponds by a diverse aquatic vegetation similarly suggests a strong seed-bank influence. Ghost ponds represent abundant, dormant time capsules for aquatic species in agricultural landscapes around the globe, affording opportunities for enhancing landscape-scale aquatic biodiversity and connectivity. While reports of biodiversity loss through agricultural intensification dominate conservation narratives, our study offers a rare positive message, demonstrating that aquatic organisms survive prolonged burial under intensively managed agricultural fields. We urge conservationists and policy makers to consider utilizing and restoring these valuable resources in biodiversity conservation schemes and in agri-environmental approaches and policies.

1. Introduction

Intensive agriculture has contributed significantly towards global habitat loss and biodiversity declines (Henle et al., 2008; Tscharntke et al., 2012). Agricultural wetlands have particularly suffered in this respect, with huge numbers of agricultural ponds and other small waterbodies lost to drainage and infilling during the last 50 years (Wood et al., 2003; Serran and Creed, 2015). Given the significant contribution of small agricultural ponds and wetlands towards regional aquatic and terrestrial biodiversity (Davies et al., 2016; Sayer et al., 2012), their widespread disappearance poses a considerable challenge for biodiversity conservation and aquatic habitat connectivity.

Many aquatic organisms have evolved strategies for surviving habitat desiccation as dormant propagules. These propagules comprise aquatic macrophyte seeds (de Winton et al., 2000), oospores (Beltman and Allegrini, 1997; Stobbe et al., 2014) and cladoceran 'resting eggs' (Hairston, 1996) that can remain viable for centuries and allow rapid species' re-establishment following habitat restoration (Beltman and Allegrini, 1997; Kaplan et al., 2014). While long-term viability of propagules has been established for extant aquatic habitats (Bakker et al., 1996; Beltman and Allegrini, 1997; de Winton et al., 2000; Hairston, 1996), their fate in 'ghost ponds', ponds that have been in-filled for agricultural land consolidation, has remained unexplored. Ghost ponds are abundant across many agricultural regions, often discernible as damp depressions or by local colour alterations in crops and soil (Fig. 2a). We investigated the restoration potential of ghost ponds, and explored the longevity and germination rates of aquatic plant propagules extracted from their sediments. With around 75% of all ponds lost across large parts of the UK since the start of the 20th century (Rackham, 1986; Williams et al., 2010; Wood et al., 2003), and with similar levels of pond loss recorded in many agricultural regions across the globe (Agger and Brandt, 1988; Curado et al., 2011; Serran and Creed, 2015), ghost ponds could represent a major and overlooked resource for the resurrection of aquatic species ostensibly lost from the agricultural landscape. Both the 'resurrection' of ghost ponds, and the translocation of their sediments to newly created sites, could provide

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highly valuable approaches in aquatic conservation. Ghost ponds have the potential to retain not only historic populations of extant species, but also remnants of flora which have become locally or regionally extinct. Further, ghost pond restoration could help to reinstate the historic landscape connectivity between aquatic habitats.

This study examined the potential viability of dormant propagules buried within the sediments of in-filled ghost ponds. External propagule sources are commonly stated as primary agents of pond colonisation (Mari et al., 2011; Williams et al., 2008), but in restored or resurrected habitats the historic propagule bank may also make a significant contribution. Focusing on three farmland ghost ponds in Norfolk, eastern England, UK, we used a multi-level experimental design to examine the longevity of viable propagules, and indicate the relative importance of the seed bank vs. external propagule sources in mesocosm colonisation. Our work establishes the viability of aquatic plant propagules following burial under intensive agriculture some 45, 50, and ~150 years ago. We show remarkable longevity of aquatic plant propagules beneath cropped agricultural fields, and highlight the great potential of ghost pond restoration for aquatic biodiversity conservation in global agricultural landscapes.

2. Methods

2.1. Experimental design

Our study comprises four complimentary approaches (Fig. 1):

i) The resurrection of three ghost ponds (Fig. 2), following burial 50–150 years ago.
ii) On-site mesocosm experiments (Fig. 3a), comparing macrophyte colonisation of 4 different treatments in four replicates, with mesocosms either open or closed to dispersal, and containing sterile or historic pond sediment.
iii) Sealed microcosm experiments (Fig. 3b), comparing macrophyte establishment from sterile and historic pond sediment.
iv) Viability testing of propagules extracted from historic pond sediments using tetrazolium chloride staining (Fig. 3c).

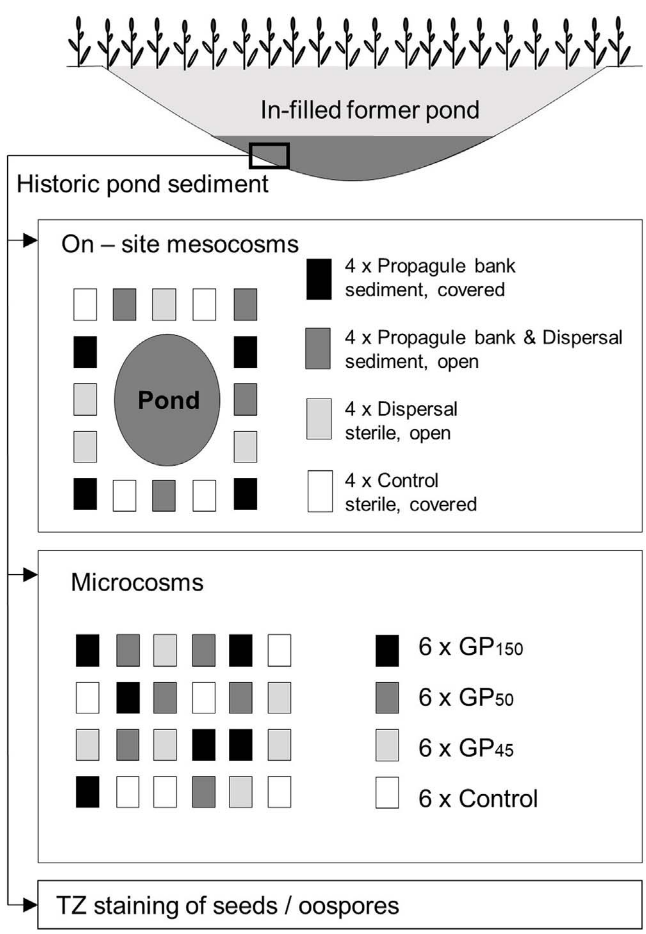

Fig. 1. Study design and experimental treatment. Historic sediment from three ghost ponds (GP_{45}, GP_{50} and GP_{150}) provided the aquatic propagule material for three different experimental treatments; on-site mesocosms (Fig. 3a), sealed microcosms (Fig. 3b), and viability testing using tetrazolium chloride (TZ) stain (Fig. 3c).

2.2. Locating and excavating ghost ponds

Ghost ponds were identified using historic UK Ordnance Survey (OS) maps and local tithe (1836–1841) maps. Within the study region of Norfolk (5371 km^2), eastern England, UK, around 8400 ponds have been lost since the 1950s. The three ghost ponds selected for this study were all located in areas that had experienced relatively high levels of pond loss: within a 3 km radius of each study pond, a further 289 (GP_{150}), 275 (GP_{50}) and 147 (GP_{45}) ghost ponds, buried since the early 1950s, were identified (Alderton, 2017). For the three studied ghost ponds, time since burial was estimated from the most recent map demarcation of a pond and from landowner knowledge of pond loss. The oldest ghost pond, GP_{150}, was buried sometime between 1839 and 1883. GP_{50} was in-filled during the late 1960s, and GP_{45} during the early 1970s. All three ponds were located on land intensively farmed over many decades. Prior to their excavation, pond GP_{150} was situated near a hedgerow, while both GP_{50} (Fig. 2a) and GP_{45} were located in the middle of arable fields.

All three ponds were excavated over September–October 2013. Once exact ghost pond locations had been established, a trench was dug through their centre and top soil was removed until dark historic pond sediments were exposed (Fig. 2b). Bulk samples of approximately 30 L of historic pond sediments were collected from multiple locations within the ghost pond basin, and stored in the dark in air-tight bags at 5 °C, prior to use in the mesocosm and microcosm experiments (Fig. 3). Each ghost pond was then fully resurrected following the profile, size and depth of the historic pond basin (Fig. 2c) and given a 6 m + marginal buffer left to natural plant colonisation. The ponds naturally filled with water over winter, and aquatic macrophytes were surveyed at weeks 5, 16, 28, 34 and 40 following excavation.

2.3. On-site mesocosms

Sixteen PVC-lined mesocosms measuring 40 × 30 × 30 cm were placed around each of the ghost pond sites (Fig. 3a). Eight mesocosms were prepared with 2 L of historic ghost pond sediment, each with 4 replicates left open to dispersal ('propagule bank & dispersal') and 4 replicates ('propagule bank') covered with 0.25 mm diameter mesh to prevent the influx of dispersing propagules. The remaining eight mesocosms were prepared with 2 L of a 50/50 mix of steam-treated potting soil and builder's sand (Boedeltje et al., 2002); with 4 again left open ('dispersal') and 4 covered with 0.25 mm mesh ('control'). Despite their small size, the positioning of mesocosms adjacent to the resurrected ghost ponds meant that waterfowl, a key dispersal vector for aquatic macrophyte seeds (Soons et al., 2016), accessed both the ponds and open mesocosms. Mallard (*Anas platyrhynchos*) were directly observed dabbling in the open mesocosms, although other bird species may also have visited the sites. All mesocosms were filled with filtered (53 μm mesh) rainwater and surveyed for aquatic macrophytes at the same time intervals as the ghost ponds.

2.4. Microcosms

Sealed microcosms were set up to corroborate the mesocosm results under strictly controlled conditions (Fig. 3b). Microcosms were set up outside at a central location situated about 25 km from the nearest