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Wetland creation and restoration for biodiversity

Outcomes of conservation initiatives to benefit birds, amphibians and occasionally fish

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Cover: Enhanced picture of Dalkarlskärret created wetland with birds, newt and fish.
(photo/drawings: I. Kačergytė)

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Wetland creation and restoration for biodiversity. Outcomes of conservation initiatives to benefit birds, amphibians and occasionally fish

Abstract

Wetlands are one of the world's most important ecosystems, but they are largely destroyed, modified, polluted and degraded. This has resulted in declines in wetland biodiversity, including that of birds, amphibians and fish. To mitigate those declines, many wetlands have been created and restored worldwide. Still, we lack large-scale wetland evaluations of the effects of wetland creation and restoration on biodiversity. In this thesis, I compared local and landscape effects to infer community responses to wetland creation. I then analysed species associations to find synergies and differences across taxonomic groups. Finally, using before-after surveys, I quantified the realised effect of wetland restoration on wetland bird communities. In general, created wetlands attracted most species of the regional freshwater community: 80% of bird and amphibian species and 50% of fish. Local habitat characteristics did relate differently to the bird, amphibian and fish community. Wetland birds were positively related to wetland size and proportion of flooded areas but negatively with the proportion of forest in the surrounding habitat. Water vegetation cover was positively associated with amphibian occurrence but negatively with bird abundance. Fish occurred more often in better-connected wetlands, while amphibians at isolated wetlands. Bird reproductive success and fish species richness was lower in wetlands surrounded by forested landscapes. It seems that several small wetlands are better for wetland bird reproductive success and similar for adult bird abundance and richness than a single large wetland. Although estimates are uncertain, the results suggest that bird-fish and amphibian-fish negative associations indicating conservation conflicts and bird-amphibian positive associations indicating a potential for bird-amphibian conservation synergies when creating wetlands. Finally, before-after surveys revealed that wetland restoration notably increased local populations of several bird species (gulls, terns, grebes, diving ducks, swans, dabbling ducks, geese, smaller waders). Nonetheless, the species-specific effects between wetlands were highly heterogeneous, and some restorations caused population declines (shrub passerines). The results of this thesis thus add important knowledge regarding how wetland creation and restoration can be improved to achieve cost-effective conservation actions to support bird, amphibian and perhaps even fish communities.

*Keywords: C*onstructed ponds, Eutrophic lakes, Freshwater vertebrates, Species associations, SLOSS, Wetland management, Re-creation, eDNA, Landscape context

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Anlagda och restaurerade våtmarker för biologisk mångfald. Analys av bevarandeinsatser för att gynna fåglar, amfibier och ibland fisk

Abstract

Våtmarker är ett av de viktigaste ekosystemen för människan. Trots detta förstörs, modifieras, förorenas och degraderas de. För att bromsa förluster av våtmarksbiodiversitet har våtmarker anlagts och återställts. Vi saknar dock storskaliga utvärderingar av vilka effekter skapande och restaurering av våtmarker har på biologisk mångfald. I denna avhandling undersöker jag hur vi kan skapa våtmarker för att gynna: i) häckande fåglar (artrikedom, antal par och reproduktiv framgång), amfibier och fiskar (förekomst och artrikedom via spår av DNA i vattnen), samt ii) om det finns möjligheter att uppnå synergier mellan dessa taxa så att högre total biodiversitet uppnås. Vidare undersöker jag om våtmarksfåglar gynnas av restaureringar genom att analysera före-efter undersökningar av restaurerade våtmarker i jordbrukslandskap i Sverige. I allmänhet attraherade skapade våtmarker de flesta av arterna från det regionala sötvattenssamhället: över 80% av fåglarna och amfibierna, över 50% av fiskarna. Våtmarksfåglar korrelerade positivt med storlek på våtmarken och andelen översvämmade ytor, men negativt med andelen skog i närliggande habitat. Vattenvegetation var positivt associerad med förekomst av amfibier men negativt med mängden fåglar. Fiskar förekom oftare i våtmarker med hög konnektivitet (via vattendrag/djupare diken), medan amfibier var artrikast i mer isolerade våtmarker. Reproduktiv framgång för fåglar och artrikedom av fiskar var lägre i våtmarker omgivna av skogslandskap. Resultaten visade också att det kan vara bättre att skapa flera små våtmarker än att skapa en stor för ungproduktion i fågelsamhället. Även om uppskattningarna är osäkra, pekar resultaten på att fisk eventuellt har ett negativt samband med våtmarkernas förekomst av amfibier och fåglar. Samtidigt är associationer mellan fåglar och amfibier huvudsakligen positiva, vilket indikerar att det finns synergier mellan dessa grupper vid skapandet av våtmarker. Slutligen visar jag att restaureringar i genomsnitt leder till ökade antal fåglar inom flera grupper (måsar, tärnor, doppingar, dykänder, svanar, simänder, gäss, mindre vadare), men till minskningar för buskhäckande tättingar. Resultaten i denna avhandling kan därmed belysa hur skapande och restaurering av våtmarker kan förbättras för att nå en mer kostnadseffektiv naturvård av fågel-, amfibie-, och ibland fisksamhällen.

Nyckelord: Skapade våtmarker, Dammar, Eutrofiska sjöar, Artinteraktioner, SLOSS, Skötsel av ängsmark, Skötsel av våtmark, eDNA, Landskapseffekter.

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Dedication

To my mother. And wildlife.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Ineta Kačergytė, Debora Arlt, Åke Berg, Michał Żmihorski, Jonas Knape, Zuzanna M. Rosin, Tomas Pärt (2021). Evaluating created wetlands for bird diversity and reproductive success. Biological Conservation, 257, 109084.

II. Ineta Kačergytė, Erik Petersson, Debora Arlt, Micaela Hellström, Jonas Knape, Johan Spens, Michał Żmihorski, Tomas Pärt (2021). Environmental DNA metabarcoding elucidates patterns of fish colonisation and co-occurrences with amphibians in temperate wetlands created for biodiversity. Freshwater biology, 66*,* 1915– 1929.

III. Ineta Kačergytė, Michał Żmihorski, Jonas Knape, Debora Arlt, Tomas Pärt. Community associations of birds with amphibians and fish in created biodiversity wetlands (manuscript)

IV. Ineta Kačergytė, Tomas Pärt, Åke Berg, Debora Arlt, Michał Żmihorski, Jonas Knape. Quantifying the effects of wetland restorations for bird communities in agricultural landscapes (manuscript)

The contribution of Ineta Kačergytė to the papers included in this thesis was as follows:

I. Conceived the project together with TP, ÅB, DA and MŻ, conducted the field study, analysed the data with support of JK and MŻ, led the writing of the manuscript and the review process.

II. Conceived the project together with TP and EP, assembled and analysed the data, led the writing and the review process of the manuscript.

III. Led the development of ideas together with co-authors, participated in data collection, analysed the data with support of JK, and led the writing of the manuscript.

IV. Participated in the development of ideas, analysed the data with JK, led the writing of the manuscript.

1. Introduction

1.1 Wetlands in modern times

Wetlands are environments for which the physical and biological properties are to a large extent influenced and shaped by water (Niering, 1985). Therefore, wetlands include a wide range of habitats, including anything from bogs and fens to saltmarsh and shallow lakes as long as it does not exceed six metres depth (Ramsar Convention, 1994). Throughout this thesis, wetlands are referred to mainly as shallow inland freshwater bodies, including natural lakes, marshes and created wetlands, some of which are ponds. In general, wetlands cover only about 8.6% of the earth's terrestrial surface (Finlayson et al., 1999) but are the most valuable ecosystems to humans (Davidson et al., 2019; Zedler & Kercher, 2005). It is estimated that out of all ecosystems globally, wetlands provide 43.5% of the monetary value of ecosystem services (109.1 trillion US dollars per year, Davidson et al., 2019). These include more than 17 ecosystem services, ranging from cultural services, such as ecotourism and landscape aesthetics, to provisioning services, such as food and peat production, to supporting services, including water storage and sedimentation (Mitsch et al., 2015). However, probably the most valuable category of ecosystem services that wetlands provide are regulatory services, making wetlands invaluable in the changing climate (Moomaw et al., 2018). These include water purification, flooding protection, climate change mitigation through carbon storage, and biodiversity (Mitsch et al., 2015). Biodiversity, in particular, is a concept that forms the basis for this thesis.

Regardless of their high value, wetlands have been extensively destroyed. Global wetland loss since the beginning of the 20th century is estimated to be

64–71% (Davidson, 2014), but these estimates differ between studies due to differences in wetland definitions, as well as geographical and temporal inclusion (Hu et al., 2017). These losses are mainly related to human activities. The main causes of wetland loss are land reclamation to expand urban areas, rising sea levels due to climate change, agricultural drainage and forestry (Zedler & Kercher, 2005). In the future, due to climate change, even protected wetlands risk being lost (Xi et al., 2020), which can be seen through, for example, an increased frequency of drought events in the USA, Australia, Middle East and Central Asia (Pekel et al., 2016).

The condition of many natural wetlands have also deteriorated (Davidson, 2014), and it is probable that mostly all wetlands are to some extent degraded (Zedler & Kercher, 2005). The causes of deterioration are linked to various human activities, including changes in river courses and damming, isolation of floodplains from water, the harvesting of wetland fauna and flora, grazing, global warming, invasive species, and other wetland modifications (Brinson & Malvárez, 2002). Even protected wetlands, such as those under the Ramsar convention, can suffer modifications due to extreme climate events, damming and reclamation (Xi et al., 2020; Zhang et al., 2021). Wetland degradation is also often related to eutrophication caused by agriculture and urbanisation (Brinson & Malvárez, 2002; Zedler & Kercher, 2005). As wetlands are usually situated in lower parts of the landscape, they are more susceptible to pollutants, which easily find their way into wetlands and accumulate there (Zedler & Kercher, 2005). Due to land-use changes, the pollutants like heavy metals and organic waste causing eutrophication might lead to species loss while promoting more common species (Petsch, 2016). Thus, ecosystem degradation can contribute to biodiversity homogenisation (Lougheed et al., 2008), which is also driven by other anthropogenic causes, affecting ecosystem functioning (Petsch, 2016). Although increased nutrient levels can have positive effects (e.g. increased primary productivity), eutrophication in shallow wetlands in agricultural landscapes can lead to decreased number of invertebrates, increased turbidity, which in turn cause further eutrophication and complete vegetation overgrowth (Lehikoinen et al., 2017). In Sweden, many wet grasslands around wetlands have transformed into reed beds, shrubberies and even forests due to eutrophication and lack of management (Hellström & Berg, 2001). This is the main cause of wetland degradation that is covered in this thesis.

1.2 Wetland related biodiversity

Biodiversity is a broad concept describing nature's variation, including differences between species, variation in genetics and functional traits (Cardinale et al., 2012). It is established that biodiversity is associated with ecosystem functioning, stability and productivity, and that when biodiversity is lost, ecosystem processes can quickly deteriorate (Cardinale et al., 2012). Currently, about 28% of assessed species are threatened globally, with the majority of these relying to some extent on freshwater habitats (IUCN, 2021; Millennium Ecosystem Assessment, 2005). The decline of freshwater fauna is directly linked to habitat destruction and degradation but is also related to pollution, habitat modifications, invasive species and overexploitation of species (Dudgeon et al., 2006). Amphibian declines, in particular, seem to be high, with 34-51% of species threatened worldwide (IUCN, 2021), and about half of all water birds are in decline (BirdLife International, 2017). Lastly, about 15% of fish species are threatened worldwide, but these estimates are generally regarded as unreliable due to insufficient data coverage (IUCN, 2021). For example, it seems that a minimum of 37% of wild freshwater fish species in Europe might be threatened, but we are aware of population declines for only 17%, while 76% of the freshwater fish species still lack data (Freyhof & Brooks, 2011). On the other hand, birds and amphibians have the best data coverage for all taxa to assess vulnerability (IUCN, 2021; Millennium Ecosystem Assessment, 2005).

These three groups of vertebrate taxa (birds, amphibians and fish) are a crucial group in freshwater ecosystems, as they contribute to many irreplaceable ecosystem functions. Wetland birds are involved in multiple ecological functions of wetlands, including population control of other species groups, such as fish, invertebrates and water vegetation (Almeida et al., 2020; Green & Elmberg, 2014). Birds respond quickly to ecological changes; accordingly, they are good indicators of wetland functioning and state of quality (Almeida et al., 2020; Fernández et al., 2005; Green & Elmberg, 2014). Amphibians also provide multiple ecosystem services, including medicine, pest control, aquatic bioturbation and are involved in multiple wetland functions, such as decomposition, consumption of primary production and nutrient cycling (Hocking & Babbitt, 2014). Similarly, fish are involved in multiple nutrient and carbon cycling processes, food web regulation and ecosystem resilience, as well as food provisioning and recreational activities (Holmlund & Hammer, 1999). Therefore, birds, amphibians and fish, in addition to their inherent ecological value, are of conservation interest due to their population declines, but fish is more often regarded in sustainable fisheries context (Cowx & Aya, 2011; Ma et al., 2010; Magnus & Rannap, 2019).

These three taxa do interact with each other, and when talking about conservation efforts to support amphibians or birds, fish are often mentioned in a potentially negative context (Brown et al., 2012; Holopainen et al., 2015). Accordingly, conservation incentives often prioritise birds or amphibians, with fish conservation only considered in special cases. Fish could be a food resource for piscivorous birds (Kloskowski, 2012; Lammens, 1999), while fish larvae could be consumed by amphibian species (Roşca et al., 2013). However, more commonly, birds and amphibians may compete for the same food resources as fish (Kloskowski, 2012; Semlitsch, 1987). Although predation by pike may threaten the reproductive success of some bird species (Dessborn et al., 2011; Paasivaara & Pöysä, 2008), amphibian predation by fish is one of the more discussed issues (Brown et al., 2012; Pope, 2008; Semlitsch, 1987). Lastly, fish consumption of invertebrates and plants might create cascading effects changing food and nesting site availability for birds and amphibians (Lemmens et al., 2013; Ortubay et al., 2006; Schilling et al., 2009). Therefore, species' use of wetland habitats may depend not only on suitable habitat availability but also on biotic interactions.

1.3 Conservation efforts to support biodiversity

Considering the ongoing loss of wetland habitat and biodiversity, conservation efforts to protect and improve wetland habitat have escalated across the world, including the Ramsar convention in 1971 and the European Union habitats directive (Council Directive 92/43/EEC of 21 May 1992). Many of these initiatives are focused on wetland birds (e.g. Bird directive, Ramsar), but also include other fauna such as amphibians. In 2005, a resolution was adopted toward sustainable use of fisheries (Ramsar Convention Secretariat, 2010), but fish diversity *per se* is rarely the primary goal of wetland protection. Currently, about 11.3% of inland wetlands are protected (by Ramsar or IUCN; Reis et al., 2017). Additionally, two other major conservation strategies have taken place. First, wetland *restoration* projects have increased (Hammer, 1997; Hellström & Berg, 2001; O'Neal et al., 2008; Moreno-Mateos et al., 2012). At least 100 million EUR has been spent for wetland restorations in Sweden so far (Pärt, 2020), while China has spent about 150 million EUR for coastal wetlands restorations alone (Fan et al., 2021). Second, wetland *creation* has increased during the last decades, especially with the goal of providing habitat for amphibians (Magnus & Rannap, 2019).

Wetland restorations are management actions to restore a wetland that has been previously drained or altered in a way that the land-use of the area has changed (Hammer, 1997), but also wetlands that have been degraded in their quality, such as in the case of eutrophication causing successional overgrowth by vegetation (Hellström & Berg, 2001; Lehikoinen et al., 2017). Restorations are usually done for several reasons, mainly for restoring water habitat after a disturbance, compensating for habitat loss, providing ecosystem services, and supporting ecosystem resilience to future disturbances (Suding, 2011). Restorations aimed at providing habitat for birds often involve water-level alterations including restored flooding regimes (Bregnballe et al., 2014; Sebastián-González & Green, 2016), management of surrounding grassland, including shrub, reed, and tussock removal, and introduced grazing, mowing or burning (e.g. Hellström & Berg, 2001; Lehikoinen et al., 2017). However, it is not always the case that restorations succeed at fully restoring previous levels of the wetlands' ecosystem functioning (Moreno-Mateos et al., 2012). Thus, restoration evaluations are essential to improve the likelihood of future restoration success. Ergo, wetland restorations are a common tool to benefit biodiversity, and large sums are invested; nevertheless, we still lack scientific knowledge about their efficiency (Lehikoinen et al., 2017).

The number of artificial water surfaces, such as water reserves or paddy fields, have increased worldwide for human convenience (Pekel et al., 2016; Perennou et al., 2012). Even though these can provide or complement the habitat for species such as birds, especially in landscapes deprived of wetlands, they cannot replace natural wetlands (Ma et al., 2010). However, the case could be different for wetlands created with the main purpose of maintaining or increasing biodiversity. Pond creation for facilitating population recovery in amphibians is a common successful conservation practice (Magnus & Rannap, 2019). Such wetlands are often small and fish-free (Magnus & Rannap, 2019), shallow, and somewhat covered by water vegetation (Brown et al., 2012). When it comes to creating wetlands for birds, it is advised that these should be larger than for amphibians but still have shallow shorelines, which enables flooding. Preferably, wetlands created for birds should contain islands or islets, with a similar proportion between open and vegetated water, and be surrounded by open meadows instead of shrubs/trees (from Swedish Environmental Protection Agency and the Board of Agriculture; Wetland Foundation and the Swedish Hunting Association; see Tonderski et al., 2002; SEPA, 2009; Feuerbach, 2014; Våtmarksfonden, 2016). However, previous research suggest that created wetlands might support fewer bird species and lower functional diversity than restored or natural wetlands (Almeida et al., 2020; Sebastián-González & Green, 2016). Therefore, there is a need to know more about the effects of wetland creation on biodiversity in order to improve their value as a tool to benefit birds and amphibians.

1.4 What do we know about the conservation intervention success?

In the case of wetland restoration for biodiversity facilitation, a set of taxa are usually used to determine the success (Sebastián-González & Green, 2016; Zhang et al., 2021). As birds are often the target taxa, it is not surprising that they are also used for restoration evaluations. Research that compared natural non-degraded with restored wetlands found that bird diversity between these two types is similar (Fan et al., 2021; Sebastián-González & Green, 2016; Sievers et al., 2018), but that the functional diversity of wetland birds might not be fully recovered (Fan et al., 2021). Most of these studies compare restored (impacted) with non-restored (control) wetlands. However, the restored and control sites could have intrinsic differences that might make the estimated effect of wetland restoration indistinct (Josefsson et al., 2020; Sievers et al., 2018). One of the reasons could be that the sites selected to be restored already hold high bird diversity values, and were therefore good candidates for restoration in the first place. Furthermore, some promising restoration projects are never realised due to flawed funding processes (O'Neal et al., 2008). The use of before-restoration surveys could alleviate such biases, but such investigations are few (Bregnballe et al., 2014; Hellström & Berg, 2001; Hickman, 1994; Lehikoinen et al., 2017; Luo et al., 2019). Before-After studies have primarily been conducted in tidal and coastal wetlands, while only three studies have investigated inland wetlands in agricultural landscapes (Bregnballe et al., 2014; Hellström & Berg, 2001; Hickman, 1994). Control sites are also important, as they help account for background population trends which could influence the estimated impact efficiency (Josefsson et al., 2020). Yet, studies that use before-after-control-impact designs are often case studies (Raposa, 2008; Rochlin et al., 2012; see also Fox et al., 2020; Mazerolle et al., 2006), but large-scale evaluations are lacking. However, these survey designs not only show how biodiversity in restored wetlands stand in relation to non-restored wetlands, but can also estimate the efficiency of wetland restorations on local population sizes and species communities, narrowing down the species groups that need better management strategies.

Generally, we lack knowledge about the effectiveness of wetland creation for biodiversity, which could help to narrow down ways to improve it. Furthermore, concerning bird diversity in created biodiversity wetlands, we generally lack knowledge about reproductive success (McKinstry & Anderson, 2002). Additionally, there is a lack of studies that examine environmental attributes and landscape context effects on wetlands created to benefit biodiversity, unlike studies investigating such associations in wetlands created for other reasons (e.g. Tourenq et al., 2001; McKinstry & Anderson, 2002; Sebastián-González et al., 2010a). Another aspect of creating wetlands is the decision of what size or how many wetlands to create, raising the question of whether a single large wetland is better than several small (SLOSS; Diamond, 1975; Simberloff and Abele, 1976), but little is known about this beyond bird species richness (Ma et al., 2010; Scheffer et al., 2006). It is well known how to create wetlands, more precisely ponds, for amphibians (Brown et al., 2012; Magnus & Rannap, 2019). However, amphibian use of wetlands created for biodiversity in general is not fully known. Moreover, fish species composition in created habitats are rarely evaluated (Kristensen et al., 2020; Langston & Kent, 1997). We lack knowledge of how fish communities in created wetlands reflect the regional species pool. As amphibians, fish and birds can simultaneously colonise wetlands and are likely to interact with one another, this might affect how the created wetland is used by some taxa (Bouffard & Hanson, 1997; Kloskowski, 2009; Kloskowski et al., 2010; Semlitsch et al., 2015), extending to the effectiveness of wetland creation as a whole. Therefore, considering species-species associations between birds, amphibians and fish in created biodiversity wetlands could indicate whether wetland use by species is affected by one another, and whether conservation synergies or conflicts could arise when considering wetland creation for multiple taxa. Answering and clarifying all these raised questions could improve outcomes for wetland conservation interventions in the future.

2. Aims

The overall aim of the thesis is to evaluate conservation interventions to facilitate freshwater vertebrate diversity. I address this in the two major types of conservation interventions made – wetland restoration and creation – and focus on three major communities: birds, amphibians and fish.

More specifically, the aims of this thesis are to:

- Examine how environmental attributes and landscape context of created wetlands associate with higher wetland use by birds and their offspring, amphibians and fish for future improvement of wetland creation (Papers I & II)
- Investigate species associations within and between fish, amphibians and birds, and to infer whether conservation synergies or conflicts may arise if wetland creation for several taxa is considered (Papers II & III)
- To quantify the effects on Swedish wetland restorations on changes in local bird population sizes (Paper IV)

3. Methods

3.1 Study sites

This thesis mostly cover wetlands in the Uppland region (59°51′29″N 17°38′41″E, Papers I - III), while the last chapter covers most parts of the Swedish agricultural landscape. Uppland is a wetland-rich region with forest-dominated areas in its northern parts, and agricultural land dominating in the southern part, of which large parts could be viewed as a mosaic landscape of forest and agricultural land. Similarly, agricultural land dominates the southern regions of Sweden, with forests dominating the north (Paper IV). Thus, *created* wetlands were located in a gradient from agriculture dominated to forest dominated landscapes, while all *restored* wetlands in Paper IV were located in agricultural surroundings (Figure 1).

The created wetlands in the Uppland region were constructed on land where, to my knowledge, no wetland previously existed. However, in some instances, a wetland existed beforehand but had been drained more than 50 years ago and been converted into arable land, pasture or production forest. Restored natural wetlands included degraded natural wetlands with the surrounding wet grasslands. Generally, degradation of agricultural wetlands was mainly caused by eutrophication and abandoned grassland management, causing the wetlands to become overgrown with tall grass, reeds, shrubs and trees.

Figure 1. Created wetlands in Uppland region, Sweden, surrounded by mostly agricultural landscape on the left and forested landscape on the right.

3.2 Data Collection

3.2.1 Biodiversity sampling

Birds, created wetlands

To gather information regarding wetland bird species richness, pair abundance, and reproductive success, several field assistants and I have performed line transect bird counts around 89 created wetlands (Paper I, but a subset of 52 was used for Paper III). All wetland bird species, except for passerines, heard, seen or flushed, were counted within wetlands and 50 meters around the wetland shore, walking at 10 min/ha speed. Thus, the effort per area was constant across wetlands. Pair abundance was estimated based on field observations of mating behaviour, while for more ambiguous situations, we followed standard methods to estimate bird pairs (Koskimies & Väisänen, 1991; Pettersson & Landgren, 2016). As some species are cryptic, we could not observe reproductive success for all species; therefore, for species such as waders and rallids, estimates on reproductive success were missing. To increase the detectability of three more cryptic species, we played audio recordings of little grebe *Tachybaptus ruficollis*, common moorhen *Gallinula chloropus* and water rail *Rallus aquaticus* (30s audio recording of species followed by listening time). To cover a larger part of the breeding season, all wetlands were inventoried four times between 14 May and 3 July 2018. Most of the inventories were carried out between 06.00 and 14.00. Each wetland was visited by more than one different observer and the timing between the visits was shuffled between wetlands such that no wetland was inventoried only during early mornings or afternoons or by the same observer. The full bird species list can be found in the Supporting information of Paper I.

Birds, restored wetlands

As Sweden has no monitoring program for restored wetlands or any standardised restoration evaluations, some of the co-authors (Tomas Pärt and Åke Berg) retrieved bird surveys from various sources, from county boards, environmental non-governmental organizations, to local birding clubs and other volunteers (Paper IV). Most commonly, parts of restored wetlands were inventoried using territory mapping, and counting observed pairs within wetlands and the surrounding wet meadows. To a lesser extent, wetland birds were counted using point counts and line transects. Even though pair abundance for various species was recorded in most cases, sometimes only individuals (two wetlands) or broods were recorded (only geese in two wetlands). The bird surveys that we were able to obtain were carried out between 1980 and 2014. Before-After restoration surveys were carried out at 37 localities (sites at 32 wetlands). Together, information about 79 bird species from a range of families was obtained, including ducks, geese, swans, grebes, waders, songbirds, finches, raptors and other species that use wetlands. However, not all wetland birds were inventoried at each locality, and often only a subset of species was surveyed. Therefore, no species were surveyed in all of the 37 localities, the most frequent being Northern lapwing *Vanellus vanellus* with 27 sites.

Figure 2. Map of SBS point count transect locations across Sweden during 1975-2019. The colours indicate how many years surveys were carried out in that area, with yellow denoting the fewest (newer routes) to the red denoting most of the years (the oldest routes). Map extracted from Green et al. (2020).

Additionally to the surveys from restored wetlands, we used bird observation data from summer point count routes from the Swedish Bird Survey (SBS; Green et al., 2020) in order to account for background national bird population trends. These point count routes are part of the Swedish bird monitoring program, which started in 1975, covering various locations in Sweden (Figure 2). Even though these routes and methods were not designed to inventory wetland birds specifically, many routes passed through parts of wetlands; thus year to year surveys could be used to obtain an estimate of population changes across years. These surveys were used to obtain reference population estimates at the national level, which mirrors the years and localities bird surveys were carried out in restored wetlands (Paper IV).

Amphibians and fish, created wetlands

Out of the 89 inventoried created wetlands, field assistants surveyed a subset of 52 wetlands for fish and amphibian occurrences using environmental DNA metabarcoding. This was done by taking water samples from 10 locations within each created wetland. The subsamples then were pooled and filtered using enclosed double filters until they were clogged. Such filters can collect tissues and other debris that contain DNA that can then be used to detect species. The DNA was then fixed, multiplied using PCR and sequenced. For this, MiFish 12S primers (Miya et al., 2015, 2020) and additionally adjusted MiFish primers to match amphibians on the 12S region were used. Finally, the obtained sequences were processed using a reference database, where species were identified for Papers II & III. The full amphibian and fish species list and other methodological information can be found in the Supporting information of Paper II.

3.2.2 Environmental data

In the field, using prepared aerial photographs, I mapped the created wetland features and vegetation cover within, and 50 m around the wetland shore (Table 1). The mapping included water vegetation (i.e. emergent and floating vegetation, wetland size, presence and area of islands, grassland cover, and tree and shrub cover). Additionally, an area that is flooded by the wetland 50 m around the wetland shore was mapped and inspected for possible hydrological connectivity, e.g. connectivity to water sources that could provide water level regulation and allow for aquatic animal colonisation. I also mapped the number of separate water pools comprising each wetland and noted whether the grassland surrounding the wetland was managed (i.e. grazing or haymaking) or not. Additionally, when the timing of wetland creation was unknown, I consulted aerial photographs (Lantmäteriet, the Swedish mapping, cadastral and land registration authority), to estimate the year or range of possible years in which the wetland was created. Lastly, I estimated landscape composition surrounding the wetland. The landscape composition investigated was the proportion of forest and urban area, which I calculated using Swedish terrain and human population density maps (GSD Geografiska Sverigedata; Statistiska centralbyrån 2019). Additionally, for Paper I only, I calculated the proportion of natural wetlands within a 3 km buffer around each created wetland (Table 1).

Table 1. Environmental variables included in the analysis for Papers I, II and III. Table adapted from Papers I & II.

Variable	Definitions	Paper	Differences
Size	Water surface, including emergent water vegetation (ha)	Papers I-III	No
Water vegetation	Cover of wetland area by emergent water vegetation (e.g. *Typha*, *Phragmites*, *Iris*, etc.) and floating water vegetation (e.g. lilies, duckweed, algae, etc.) (%)	Papers I-III	Paper I only emergent water vegetation
Open islands	Area of constructed islands covered by grass vegetation or bare soil (ha)	Paper I	
Wooded islands	Area of constructed islands that were covered with bushes and trees (ha)	Paper I	
Number of ponds	Number of separate created water bodies (pools) in a wetland complex	Paper I	
Flooded area	Adjacent area that can be flooded (%), defined by soil humidity and vegetation (50 m buffer surrounding the water surface shore)	Papers I-II	Not applied for fish, Paper I included only flooded wet meadows
Local forest	Adjacent area with trees and bushes (%) (50 m buffer surrounding the wetland shore)	Paper I	
Management	Presence of management (e.g. vegetation management).	Paper I	
Year of creation	Year wetland was created.	Papers I-II	Not applied for amphibians
Inflow	Whether wetland is hydrologically connected (yes/no) providing water influx (ditches, streams, water pumps (latter just 2 cases)), so that water levels are less dependent on rain	Paper I	
Connectivity	Whether the wetland has ditches/streams that connect it to other water bodies (except for dams)	Papers II-III	No
Landscape forest	Coverage of forest within 1 km buffer starting from the wetland shore (%)	Papers I-III	Paper I, starting from 50 m buffer
Urban area	Area with at least one registered person living (100 m^2 resolution) within 1 km buffer extending from the 50 m buffer surrounding the shore (%)	Paper I	
Neighbouring wetlands	Area of water bodies within 3 km buffer extending from the 50 m buffer surrounding the shore (%)	Paper I	

3.3 Study design

3.3.1 Created wetlands

I selected the study wetlands from the pool of all wetlands constructed directly for biodiversity in the Uppland region (Dietrichson, 2017). Wetlands were selected randomly, but in a stratified way. This was to ensure that no environmental attributes would have been over-represented across wetlands; ensuring that size, amount of separate pools within the wetland, amount of local and landscape forest, represented an environmental gradient from wetland to wetland (see Paper I methods).

3.3.2 Restored wetlands

I used data from all known wetland restorations in Sweden that had bird surveys from both before and after wetland restoration when going through all collected data from various sources. The use of before-after restoration bird surveys enables direct estimation of the change in abundance following restoration interventions. Additionally, I used the SBS dataset to compare SBS point count surveys from the same years that the surveys in restored wetlands were carried out. Therefore the SBS dataset served as a control to account for background population trends at the national level. Even though this is not a conventional contrast analysis, data treated in such a way could be interpreted as Before-After-Control-Impact design (BACI, Paper IV).

3.4 Data handling and analyses

3.4.1 Environment and biodiversity correlates

Throughout all chapters in the thesis, generalised linear models (GLM) and generalised linear mixed models (GLMM) are the most common tools used to assess the relationship between environmental data and biodiversity responses. GLMs were commonly used to assess the environmental impact for species occurrences (Papers I & II) and richness (Papers I & II) as well as changes in abundances of individual species (Paper IV). GLMMs were used on occasions for analyses of pair and chick abundances (Paper I). Using species identity as random effects allowed the modelling of community-level responses that are not entirely driven by the most common species and allowed the rarer species to have higher contributions to the model estimates. Although the mean responses might be not as straightforward to interpret, the linear change display a more representative community-level response.

3.4.2 Species-species co-variances

I estimated species co-occurrences and co-variances in Papers II & III using two different statistical tools. In Paper II, species-species associations were estimated using the probabilistic species co-occurrence model (Griffith et al., 2016). This modelling approach compares observed co-occurrences to expected co-occurrences under random species co-occurrence assumptions. Such analyses provide an overview of species distributions and indicate potential species avoidance, exclusion or attraction. However, this tool has limitations, as only occurrence data can be used, and species niches driving some species co-occurrences are not accounted for. As such, I used a joint species distribution model approach implemented in the HMSC package (Tikhonov et al., 2020; Paper III). This modelling framework estimates species-specific responses to the environment and, simultaneously, co-variances among species across habitat patches (i.e. wetlands). Abundance data holds more information than only occurrences (Blanchet et al., 2020), making better use of the data collected and potentially increasing statistical power for detecting species-species associations. Thus, I modelled fish (seven species) and amphibian (five species) occurrences along with bird pair abundances (14 species, see Paper III), and then fish and amphibian occurrences along with bird chick abundances separately (five species, see Paper III). After estimating the species-environmental responses (i.e. abiotic filtering, Ovaskainen & Abrego, 2020), the remaining species distribution variances were then used to calculate the species-species co-variances. However, the estimated associations can be dependent on other environmental factors driving these patterns that I did not account for. In general, inferring biotic interactions from species co-occurrences are often impossible, as multiple factors might affect the estimated signals (Blanchet et al., 2020). Accordingly, the results of both methods can only be used to reflect species-species association in sparse ecological data.

3.4.3 Approach to deal with heterogeneous bird surveys from restored wetlands

In Paper IV, I had to deal with highly heterogeneous data. To approach this problem, I analysed the change in bird abundances between before and after the restoration for each site and species separately using simple GLMs. For this analysis, I used only 28 sites and 68 species (see Paper IV methods, species gains and losses, and sites with less than three inventories removed). The simple GLMs allowed me to estimate restoration effect sizes for each site and species independently of their abundances and methods used; thus, the effect sizes were standardised across the wetlands, and show the relative change in abundances after the restoration (log-ratio change). In this way, the restored wetlands and bird observations retrieved from SBS were used to calculate the magnitude of changes in impacted (restored wetlands) and “control” sites (SBS dataset). Lastly, to approach this data similarly to a BACI design, I subtracted the effect sizes of SBS data from the restored wetlands:

$$\text{Contrast}_{\text{effect\_size}}=\text{Impact}_{\text{effect\_size}}-\text{SBS}_{\text{effect\_size}}$$

These standardised contrasted effect sizes, together with their standard errors, were used to quantitatively estimate the effect sizes across species and wetlands using meta-analyses tools with the metaphor package (Viechtbauer, 2010). Meta-analysis is a statistical method to quantitatively summarise the results across heterogeneous studies, and offers a way to combine the outcomes of various sources into one (Harrer et al., 2021). All analyses and visualisation in this thesis were done in R (R Core Team, 2019).

4. Results and Discussion

4.1 Species use of created wetlands and their relation to environmental attributes

The 89 created wetlands in Uppland, Sweden, provided breeding habitat for 38 out of the 45 wetland bird species in this region (excluding passerines; Paper I; Ottosson et al., 2012). Additionally, the 52 created wetlands analysed using eDNA metabarcoding provided suitable habitat for all five amphibian species of this region (except pool frog *Pelophylax lessonae,* which breeds outside the sampling area along the coast). Lastly, out of the 32 fish species residing in the region, 17 fish species were detected in the created wetlands (Paper II). The reason for some species not being observed could be the individual taxa needs for size and depth (Muus & Dahlström, 1972; Nilsson, 1986). As beta diversity for birds and especially fish species is quite high, it is possible that more species would have been found in created wetlands if more sites had been examined (Figure 3).

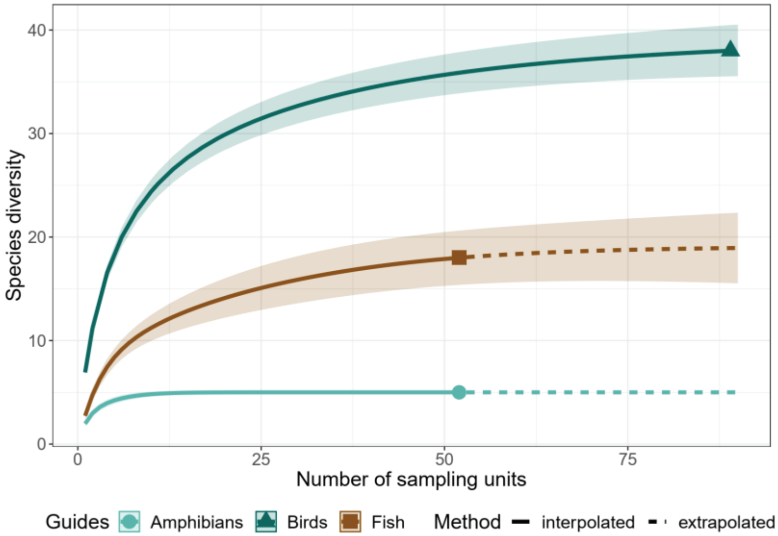

Figure 3. The sample size based rarefaction-extrapolation curve (90 sites, iNEXT R package, Hsieh et al., 2016). The lines represent diversity estimates as a function of the number of wetlands with 95% confidence intervals (CI).

4.1.1 Local environmental attributes

Higher bird species richness and pair abundance was associated with larger wetlands (Paper I, Figure 4a), in line with island biogeography theory and previous wetland bird research (Froneman et al., 2001; Sebastián-González & Green, 2014). However, pair abundance was lower in wetlands overgrown by emergent water vegetation (Paper I, Figure 4a), while a higher cover of water vegetation was associated with higher amphibian species richness and occurrence (Paper II, Figure 5). Although emergent water vegetation was related negatively to pair abundances, water vegetation is an important element for amphibians. Water vegetation could help amphibians hide from predators and be important for breeding (Shulse et al., 2012). Although birds should benefit from water vegetation for similar reasons as amphibians (McKinstry & Anderson, 2002), the negative association of bird abundance and water vegetation could be related to decreased detection probability, but also to reduced amount of habitat for foraging and nesting (Ma et al., 2010).

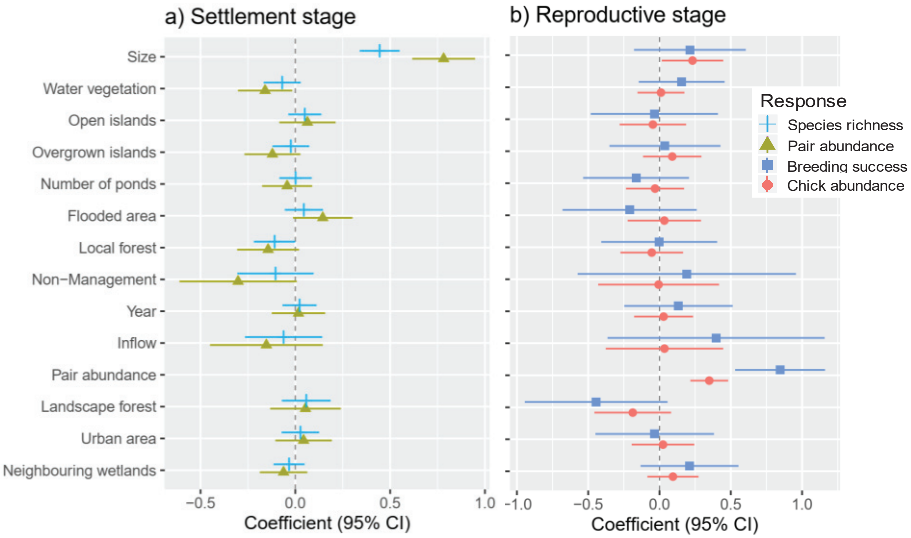

Figure 4. Model coefficients and confidence intervals explaining variation in species richness (turquoise line), pair abundance (khaki, triangles), breeding success (blue, squares) and chick abundance (red circles). All predictors are centred and scaled; size and pair abundance are log- and islands square-root-transformed. This figure is adapted from Paper I.

Bird pair abundance was greater in wetlands with a higher proportion of grasslands that were flooded during spring (Paper I, 50 meters around the wetland shore), but unlike previous research suggesting positive associations with flooded areas (Brown et al., 2012), amphibians did not relate to the flooded area (Paper II). Birds benefit from the flooded areas due to the increased amounts of foraging habitat they create (Milsom et al., 2002; Żmihorski et al., 2016), while amphibians should have benefited due to refuges from predatory fish (Porej & Hetherington, 2005). Additionally, bird species richness was lower in wetlands that were surrounded by nearby trees and shrubs (Paper I, Figure 4a). Such bird diversity response to trees could be related to potential avian predators using these as perching posts (Berg et al., 1992; Holopainen et al., 2015), and reduced nutrient levels in the wetland (Licht, 1992).

Although birds were not related to connectivity measures (Figure 4, see Paper III), fish species richness was two times higher in connected wetlands than in isolated ones, while amphibian species richness was 40% lower (Figures 5-6, Paper II). It seems that the presence of connectivity to other water bodies is the main driver of a higher probability of fish species occurrences, as this allows for natural fish colonisation (Novinger & Rahel, 2003). Nevertheless, isolated wetlands still contained fish, probably due to recreational fish stocking (Paper II, Spens & Ball, 2008). On the other hand, higher amphibian occurrence and richness in isolated wetlands is probably not attributed to environmental preferences but to fish avoidance or exclusion (see 4.2).

The desired conservation outcome from wetland creations could be how reproductive success stands in relation to the long-term success of wetland creation actions, and for stability in the regional species pool. Therefore, investigating the environmental constraints for reproductive success in created wetlands is important. It seems that in general, high reproductive success mainly depends on high abundance of adults; consequently, directing conservation strategies to support adults will benefit reproductive success, too (i.e. chick abundance, Figure 4b, Paper I).

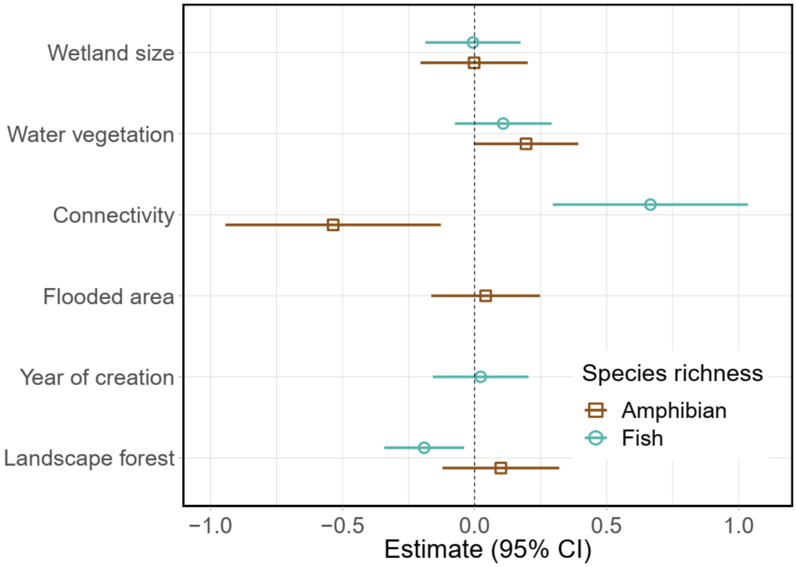

Figure 5. Amphibian and fish species richness relation to the environmental variables (mean centred and scaled), expressed by the model estimates and 95% confidence intervals. Wetland size was log-transformed. This figure illustrates results from Paper II.

4.1.2 The importance of landscape composition and spatial scale

Fish species richness and reproductive success of wetland birds were lower in wetlands surrounded by forested landscapes (Papers I & II, Figures

4b & 5). The most obvious reason for such a pattern could be the reduced food availability in oligotrophic conditions, something that is common in boreal forest landscapes such as those in Uppland (Holopainen et al., 2015). These conditions could also create higher competition between fish and birds foraging on invertebrates, thus lowering chances of chick survival (McParland & Paszkowski, 2006; Nummi et al., 2012). However, landscape composition did not seem to associate clearly with amphibians and adult wetland birds.

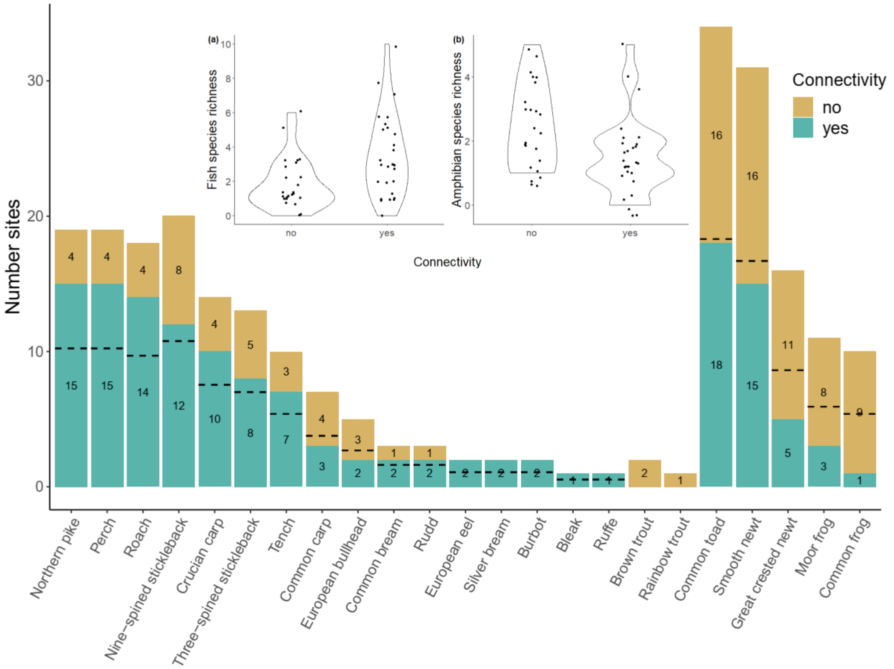

Figure 6. Fish and amphibian species occurrences in connected (turquoise) and isolated (dark yellow) wetlands with black lines indicating the expected number of occurrences under random distributions. The violin plot (a) depicts fish species richness and (b) amphibian species richness. This figure is adapted from Paper II.

I also investigated a classic conservation question on whether single large or several small habitat patches is better (Diamond, 1975; Simberloff & Abele, 1976) in the context of wetland creation for birds. Although larger wetlands contained more pairs and bird species locally (Figure 4a, Paper I), many small wetlands had a similar number of species compared to one large at the regional scale (Figure 7a; see also Brown & Dinsmore, 1986; Craig &

Beal, 1992; Scheffer et al., 2006). After scaling up the model predictions of various wetland sizes to match the size of the largest one, I found that several small wetlands together to have similar pair and higher chick abundances than a larger wetland of the same total size (Paper I, Figure 7b-c). This can be attributed to the increased habitat heterogeneity that comes with having several different wetlands, thus benefiting many bird species covering multiple niches (Fahrig, 2020; Ma et al., 2010). However, for this argument to hold, one would have also expected to see higher species richness in the combination of smaller wetlands. A higher total wetland perimeter could also contribute to observed pattern, as many birds forage on the shore, hence many smaller wetlands would increase the amount of habitat (Eriksson, 1983; Nilsson, 1986).

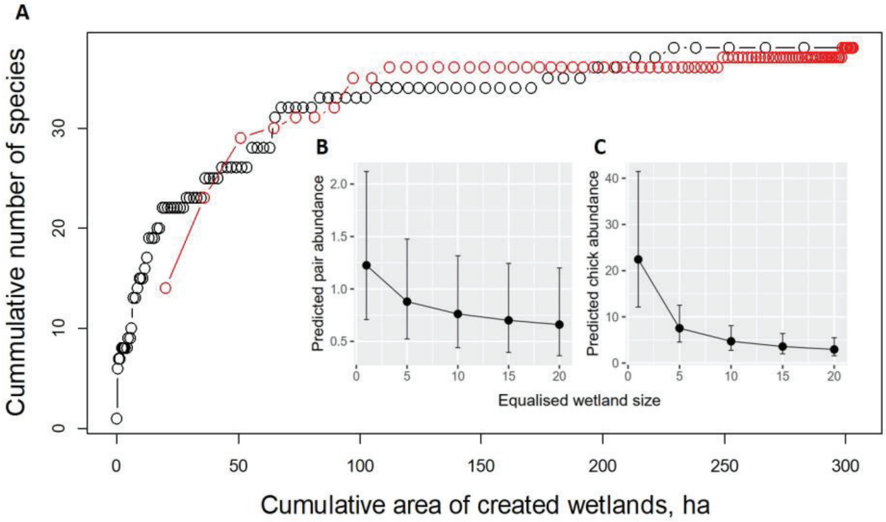

Figure 7. SLOSS comparison. A) Cumulative species richness as a function of cumulative area of created wetlands included. Black circles indicate accumulation direction from smallest to largest wetland, while red - from largest to smallest. B-C, a comparison of estimated effects of single large or several small wetlands on the abundance of pairs (B) and chicks (C) for multiple wetlands of different sizes, making up a total of 20 ha. The predicted pair and chick abundance when controlling for species and site identity and environmental variables (but not controlling for pair abundance in the analyses of chick abundance). Error bars refer to 95% confidence intervals. (Adapted from Paper I).

4.2 Associations between birds, amphibians and fish

It is a common notion that fish have a negative effect on amphibian populations (Brown et al., 2012; Heyer et al., 1975; Porej & Hetherington, 2005). However, fish and amphibians did co-occur in 85% of the 52 investigated created wetlands (Paper II). Nonetheless, this number is only 60% if we would consider the more susceptible frog and newt species without the common toad *Bufo bufo,* which is a species that is not usually affected by fish depredation due to its toxicity (Beebee, 1979; Manteifel & Reshetnikov, 2002). On the other hand, connected wetlands had higher fish occurrence rates and species richness than isolated wetlands, while amphibian species richness and occurrence were lower in connected than isolated wetlands (Figure 6). The different effects of wetland connectedness between amphibians and fish could imply that there might be some amphibian avoidance of wetlands that contain fish. Additional analyses in Paper II also imply that some amphibians and fish did co-occur less often than expected by chance, but such examples were few. Therefore, whether these results support the general notion of negative fish effects on amphibians are not straightforward. Such results showing more neutral fish-amphibian associations have been found elsewhere, at least for native fish species (Pearl et al., 2005), although it is not common.

According to the results of the joint species distribution modelling, there were very few species-species co-variances between fish, amphibians and birds whose 95% credible intervals did not include zero after some abiotic interactions are accounted for (Figure 8). Apart from some positive within-bird and within-amphibian species associations, cross-taxon associations included those between amphibians (except the toad) and a few species of birds (common goldeneye *Bucephala clangula,* moorhen and teal *Anas crecca* pairs, and goldeneye chicks, Figure 8, Paper III). Additionally, the general pattern indicates mainly positive, despite not statistically clear (i.e. 95% CI include zero), associations between amphibians and birds, especially with dabbling ducks. Although some bird species can predate upon amphibians (Kloskowski et al., 2010), previous research indicates that amphibians and birds respond similarly to the presence of fish and wetland management (Ortubay et al., 2006; Tozer et al., 2018). Therefore, these results could indicate that joint wetland creation for birds and amphibians could be a possible conservation strategy, but further research may be needed (e.g. negative association of amphibians with common crane *Grus grus*).

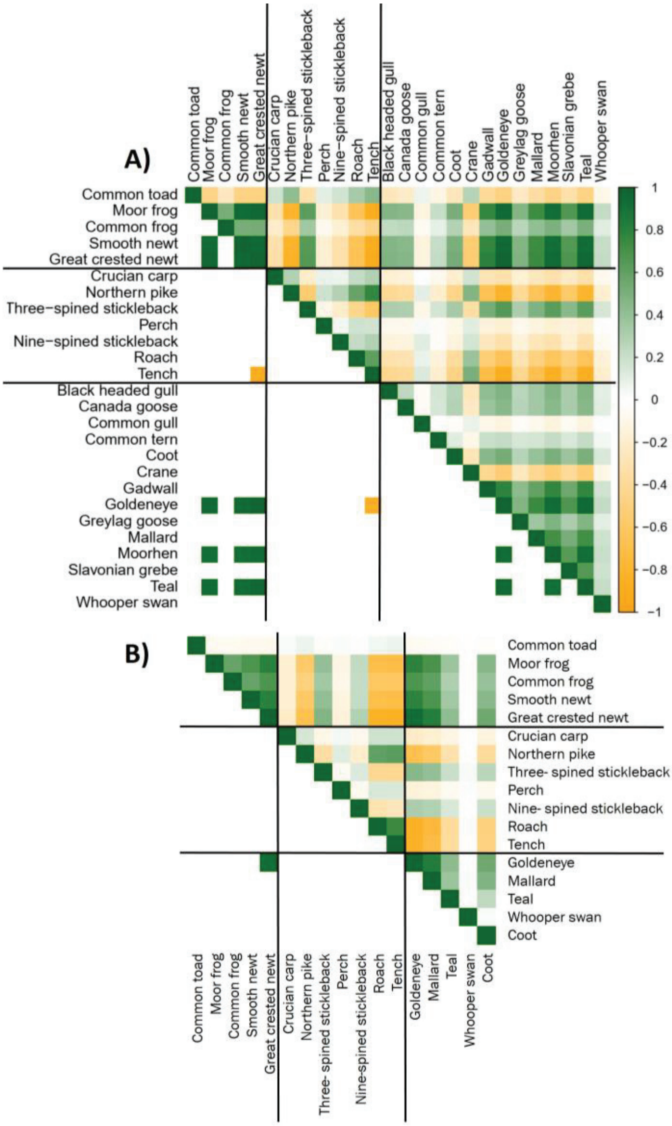

Figure 8. All species-species associations were measured at the wetland level using a model with environmental variables (wetland size, water vegetation, connectivity and landscape forest) in the joint species distribution models (HMSC R package). The models include ordered species measured as occurrences for amphibians and fish, and bird abundances of A) pairs and B) chicks. The coloured squares indicate the estimated species-species association parameter values (correlations at the scale of linear predictors) as labelled by the scale, either positive (green 0 - 1) or negative (yellow -1 - 0). The bellow diagonal part of panels indicates species associations whose 95% credible intervals do not include zero (see Paper III for more details), while above diagonal all species-species association point estimates are shown. Adapted from Paper III.

There were no clear species-species co-variances regarding bird-fish species except for a negative association between goldeneye pairs and tench *Tinca tinca* (Figure 8a). However, the general patterns indicate possible negative associations between fish and bird community, especially with dabbling ducks (Figure 8, Paper III, but see three-spined stickleback *Gasterosteus aculeatus*). Several studies have shown negative duck-fish species associations due to direct predation or possible competition (Dessborn et al., 2011; Eadie & Keast, 1982; Nummi et al., 2012; Paasivaara & Pöysä, 2008; Väänänen et al., 2012), but the results from Paper III did not provide clear support for such associations.

The reason for an absence of a clear negative amphibian-fish and bird-fish association, as has been shown in previous studies, could be the survey method used. While many other studies used mainly field observations, funnel traps and multi-mesh gillnets (e.g. Porej & Hetherington, 2005; Magnus & Rannap, 2019), the occurrence data for Papers II & III was obtained using eDNA metabarcoding. It seems that the multi-mesh gillnet method often misses smaller fish species (Sutela et al., 2008), while eDNA metabarcoding itself should not have such bias and actually has quite high fish species detectability (Fujii et al., 2019). The lack of clear bird-fish-amphibian associations could be due to lack of statistical power to detect the associations. The low power could arise from that fish and amphibian occurrences conveyed less information than abundance or biomass estimates would, and that 52 sites might be not enough to detect weaker associations in the sparse ecological data. Additionally, negative fish-amphibian and fish-bird associations are usually detected by contrasting fish-free water bodies with wetlands where fish were present (Elmberg et al., 2010; Haas et al., 2007; Pope, 2008; Porej & Hetherington, 2005), whereas fish were detected in all but three of the 52 created wetlands. Together with the use of a one-year survey (see Sebastián-González et al., 2010b), this could make detecting potential exclusion, avoidance or attraction harder. In addition to the low power to detect clear species co-variances, most studies showing negative bird-fish associations have been conducted in oligotrophic systems (McParland & Paszkowski, 2006; Nummi et al., 2012), while it has been suggested that wetlands that are rich in food resources would be able to maintain competing species populations (Eadie & Keast, 1982). This could be the case for some created wetlands located at agricultural landscapes in Uppland region. Nevertheless, the results of Papers II-III suggest that co-existence between birds, amphibians and fish is frequent in the created wetlands, despite amphibian avoidance or exclusion from connected, fish rich wetlands and the general pattern of seemingly negative bird-fish estimated associations.

4.3 Effects of wetland restorations on birds

A clear pattern of wetland bird population increase was revealed in about half of the wetland bird species when comparing the local population changes of wetland birds before and after wetland restoration (Paper IV, Figure 9). Analyses from Paper IV lend support to wetland restoration success in four groups of birds investigated. These included species such as gulls and terns (island breeders), grebes and diving ducks (deep water foragers), grey heron *Ardea cinerea*, swans, dabbling ducks (shallow water foragers), geese, smaller waders, meadow pipit *Anthus pratensis* and yellow wagtail *Motacilla flava* (short meadow breeders, Figure 9). These species could have generally benefited from the restoration measures applied in these wetlands, including restored or increased water levels (Ma et al., 2010), reed management by cutting or removing with roots, mowing and grazing of the surrounding wet grasslands and shrubs to increase the openness of the surrounding grasslands (Lehikoinen et al., 2017). The increase in bird abundances following wetland restoration justifies wetland restorations as a valid tool to conserve wetland birds, despite the observed and expected decline of shrubland breeders (11-59% decline, Figure 9). These passerines (shrubland breeders) show mainly negative responses because wetland restorations most often involve measures destroying their breeding habitat (Lehikoinen et al., 2017), as overgrowth by trees and shrubs is often a sign of wetland degradation. However, the expected outcome from restorations for wetland species may vary substantially as shown by high species- and site-specific variation in restoration effects, making future restoration efficiency hard to predict. This high variation of species-specific responses between wetlands could be caused by many factors, spanning from species biology and pre-restoration conditions, to the actual extent and number of restoration measures taken. However, such species-site heterogeneity could also be due to the lack of standardised wetland bird inventories, as the bird surveys used for Paper IV varied greatly in sampling and survey design. Such variation in effect sizes between wetlands due to heterogeneous sampling across wetlands could arise from varying detection probabilities, the area of the wetland inventoried, the survey effort (see Ruete et al., 2020) and limited sample size (Lajeunesse, 2015).

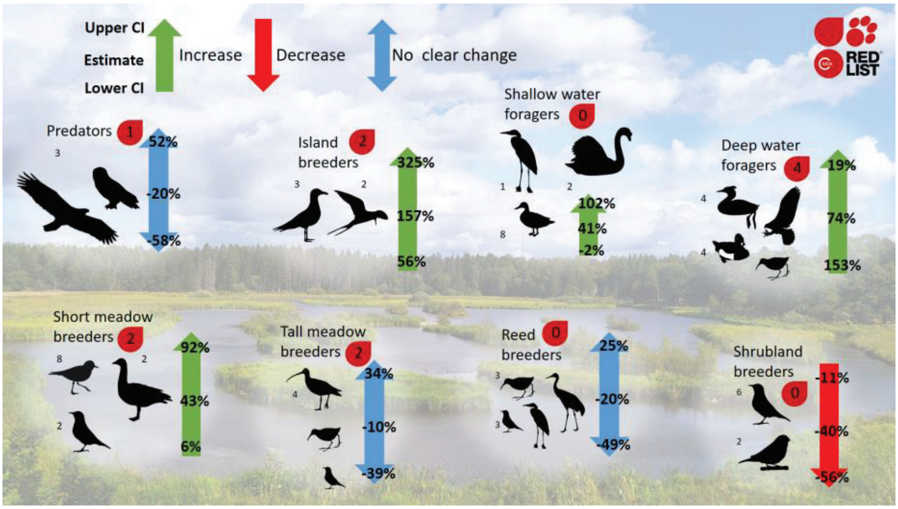

Figure 9. Group responses to wetland restorations based on the species-site-specific change in abundance following restoration, after accounting for national bird population trends. Numbers show the span and mean change of each species group (Estimated mean population change and 95% Confidence Intervals). The bird shadows depict a family of species included (digits indicate the number of species included), while the red drop indicates the number of threatened species (species classified as Least Concern, Near Threatened, Vulnerable, IUCN 2021).

5. Conclusions, management implications and future perspectives

In light of freshwater biodiversity often facing the highest declines compared to other biomes (Millennium Ecosystem Assessment, 2005), effectively executed conservation measures can be the key for the promotion of biodiversity (Amano et al., 2018). However, we need to understand better how conservation efforts to provide habitat could be more efficient to ensure positive outcomes. In this thesis, I assessed the wetland creation and restoration strategies for facilitating positive biodiversity outcomes in wetland birds, but also amphibians and fish. This made it possible to reveal potential knowledge gaps and to suggest future wetland creation and restoration directions for this highly diverse set of species.

5.1 Wetland creations for wetland birds, amphibians and occasionally fish

5.1.1 Bird, amphibian and fish community associations with environmental attributes

I found that overall, created wetlands are valuable for promoting wetland birds, amphibians and even fish, regardless of the wetland size. The results from Paper I coincide well with the current guidelines of wetland creation for birds in Sweden. This includes the creation of larger wetlands with managed water-vegetation cover (allowing some, but not high coverage), a lower proportion of tree and shrub cover around the wetland, as well as creating wetlands with gradual shorelines allowing water to flood into the surrounding areas (see section 1.3). As for the five amphibians residing in the Uppland region, water vegetation and wetland isolation from other water bodies would facilitate their occurrence. Furthermore, fish were more likely to be found in wetlands that were connected with other water bodies as well as wetlands not surrounded by a high proportion of forest. In fact, landscape composition, more specifically the proportion of forest, might be as negatively related to fish as to the reproductive success of birds. This suggests that creating wetlands in forested landscapes might not be as beneficial for multiple taxa compared to locating wetlands in less-forested landscapes. Lastly, one of the more practical suggestions arising from my thesis is that creating several small wetlands at the landscape scale is as good, and in some instances even better, than one large wetland locally for the bird community. Analyses in Paper I indicate that wetland bird population sizes and reproductive success also benefit from the creation of small wetlands, in addition to the evidence that several small wetlands hold similar levels of species richness to single large (Fahrig, 2020). As land must be spared when creating new wetlands, such a result encourages creating wetlands of any size, adding to the regional pool of species diversity.

Especially with Paper I, I provide an overview of the relative importance of environmental variables that are likely to positively affect wetland birds and their offspring. Although I do not advise to use such models predictively, they narrowed down which environmental variables are important for wetland birds, thus pinpointing the most influential aspects when constructing wetlands and prioritising candidate sites for wetland creation. However, the scope of this thesis did not give time to explore the possible effects of interactions between environmental variables on bird, amphibian, and fish communities. In particular, the amount of forest in the surrounding landscape could have interactive effects with water vegetation or wetland size on the bird community, affecting food availability or predation pressures. Therefore, future research should investigate whether such interactions exist and identify the reason behind such associations.

Lastly, to my knowledge, several wetlands that were created in the Uppland region to promote biodiversity have been drained. Thus, the investment for facilitating birds have been lost. Hence, funding bodies and environmental protection agencies could suggest that landowners apply for additional funding for land sparing of created wetlands. Furthermore, additional support for management of created wetlands is needed, as these may degrade over time.

5.1.2 Potential for conservation synergies and conflicts between birds, amphibians and fish

Concerning bird, amphibian and perhaps fish facilitation from wetland creation, possible expected synergies and conservation conflicts can be predicted from the general patterns identified in this thesis. I found a lack of clear evidence for species-specific bird-amphibian exclusion or avoidance, as most associations were positive and some statistically clear. This indicates that joint facilitation of birds and amphibians by wetland creation may be a possible topic for further consideration. The fish community, on the other hand, is another issue. Except for three wetlands, all had fish, and only two fish species detected are of conservation interest (European eel *Anguilla anguilla* and *wild* Common carp *Cyprinus carpio,* IUCN 2021). Although not statistically clear, the overall patterns of bird-fish and amphibian-fish co-variances indicate negative species associations. Based on Papers II & III and other studies (see reviews Brown et al., 2012; Holopainen et al., 2015), it would be wise to create wetlands for amphibians and birds that would be less readily colonisable by fish. This could be achieved by creating isolated wetlands or providing information signs to discourage fish stocking. However, more research must be done before a clear conclusion for conservation strategies can be achieved. As experimental studies might be impractical for such large communities, future research thus needs to include broader geographic and temporal coverage, increasing the sample size. Additionally, occurrence data of fish and amphibians might not be sufficient for detecting clear species-species associations. Therefore, future development in eDNA metabarcoding could ease wetland sampling and might elucidate the patterns of bird-fish-amphibian associations, as there is evidence that biomass or abundance of at least fish could be estimated using eDNA under certain conditions (Rourke et al., 2021).

5.2 Wetland restorations for birds

Wetland restoration for birds seemed to be successful for half of wetland bird species, although some species did not clearly benefit. The present data did not allow me to investigate which current restoration measures are beneficial for groups of species or specific species and for which species it may be harmful, especially for species of conservation concern, such as black-tailed godwit *Limosa limosa* or curlew *Numenius arquata*. However, the estimated effect sizes in Paper IV can help answer future questions and help improve the efficiency of wetland restorations. This includes identifying species vulnerable to restoration and species in need of improved restoration measures, and setting targets for future restoration efficiency.

In the future, we need to determine the mechanisms behind successful wetland restorations. As birds are mobile, and most of the wetlands in Sweden are not isolated, we must consider metacommunity dynamics. In the case of wetland restoration, I would be interested in testing the wetland-wetland dynamics based on the mass effects framework. Mass effects are, simply described as source-sink dynamics between populations, created by dispersal among habitat patches of varying quality when gamma diversity is moderate (Leibold & Chase, 2018). Here several hypotheses could arise. First, suppose wetland restorations are successful through enhancing local population breeding success by increased habitat quality. In that case, one could expect restored wetlands to act as a source community, increasing populations also in the surrounding wetlands. If this is true, then determining restoration efficiency only locally might underestimate the true benefit of wetland restorations. Second, the opposite could be hypothesised. If wetland restorations only increase the attractiveness of a wetland but not habitat quality, then neighbouring wetlands could lose individuals. Thus, estimates of restoration effects would be driven mainly by immigration. This could happen due to, for instance, increased predation rates, making the restored wetland into a sink habitat (i.e. ecological trap or nonideal habitat, Battin, 2004; Arlt & Pärt, 2007). Third, one could also hypothesise that restored wetlands could act as sinks during the first years of restoration but become sources after some years. It would require extensive effort to collect the data to determine whether restoration effects are visible not only at the local but also at the landscape scale. A possible solution to bird data limitation across spatial and temporal scales could be to use abundant, if available, citizen science data to cover before- and after- restoration observations of wetland birds in both restored and non-restored wetlands (e.g. Swedish species gateway, ArtPortalen; for applications, see Ruete et al., 2017).

The synthesis in Paper IV highlighted that restored wetlands generally lacked unifying survey methods, and only the minority of restored wetlands had the desired before-after surveys, but no accompanying surveys of a non-restored (control) wetland. Even if it feels unnecessary, control sites are needed to relate the estimated effect sizes of restored sites to account for processes unrelated to restoration (Josefsson et al., 2020; Sievers et al., 2018). As future studies may face similar issues regarding lack of data and data heterogeneity to evaluate restoration success, we need to have standardised bird surveys for restored wetlands (for similar issues and solutions, see Hellström & Berg, 2001; Żmihorski et al., 2016; Josefsson et al., 2020, 2021). The support and guidelines for surveys can essentially be provided by funding bodies and environmental protection agencies. Wetland biodiversity losses can be undetected in regions where biodiversity monitoring is not common (Amano et al., 2018); thus, encouraging frequent standardised bird surveys can improve our understanding and future outcomes of wetland restorations. Such surveys should include several years of before and after restoration inventories, as well as control sites. An alternative could be to use other data sources, such as those used in Paper IV or opportunistic citizen science data (e.g. ArtPortalen). However, these kinds of data have a number of issues, as they were not designed for such purposes and thus are likely to be less reliable than surveys designed to monitor the outcomes of wetland restorations.

5.3 Conclusions

In conclusion, this thesis reveals fish, amphibian and bird communities' use of created biodiversity wetlands and how these reflect regional species pools. Together with the co-authors, I have demonstrated which environmental attributes, at local scales and within a landscape context, are associated with breeding bird, amphibian and fish rich wetlands created for biodiversity. I also discussed possible conservation conflicts and synergies between birds, amphibians and fish, and indicated future research directions. Lastly, I have estimated the contribution of wetland restorations for species population growth across the whole wetland bird community. Results indicated restoration benefit for half of the bird community, but it is clear that more research is needed, including studies using Before-After Control-Impact designs across the local, landscape, and temporal scales. Thus, my thesis can help to direct future research and conservation strategies to improve freshwater habitat for multiple vertebrate taxa, something that could benefit humans and wildlife across the globe.

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Popular science summary

Wetlands are one of the most important ecosystems to humans and wildlife. They provide food, habitat for animals and protection from flooding. They help to tackle climate change, and are lovely places to spend your free time. However, during the last hundred years, we have drained more than half of wetlands for agriculture, mining and forestry. Wetlands have also been modified for our urban lifestyles, and we have polluted them with agricultural and urban waste. As a consequence, many remaining wetlands have become degraded and do not look healthy. Consequently, animals that use wetlands as their home, including the birds, amphibians and fish covered in this thesis, have experienced negative effects of these changes during recent decades. However, these three groups of animals are essential for maintaining a healthy and thriving wetland ecosystem. Therefore, conservation efforts, including the conservation of remaining wetlands, and the (re-)creation of new wetlands, have been applied to help populations of birds and amphibians, and to a lesser extent, fish. These conservation efforts first started to appear around 30-40 years ago and have since bloomed into solid support for wetland species today.

Despite these well-meaning actions, there are several things we do not fully understand about wetland creation and restoration for increasing animal diversity. In general, we lack knowledge about what happens in different types of wetlands in the years after it was restored or created, especially regarding the species they are designed to protect. Therefore, I assessed the restoration success in 37 restored wetland locations across a range of Swedish agricultural landscapes using existing bird observations from before and after the wetland was restored. Because these observations were made by bird watchers voluntarily without a common method across surveyed wetlands, I used advanced analytical tools to account for the potential problems that can arise from using such "messy" data. I also considered each species' national bird population trends so that the calculated benefit of wetland restoration would be less likely influenced by other factors not related to the restoration itself. Although creating or improving habitat should benefit local biodiversity, we do not have much evidence regarding how fish, birds, and amphibians actually respond to these conservation actions. It may be hard for newly-created wetlands to uphold diversity values similar to natural wetlands, but we can still learn and improve their creation and management to achieve the best outcomes possible for biodiversity. An assessment of which characteristics that created wetlands need to best help animals during their breeding time should help them thrive in the long term. Therefore, I also carried out some targeted surveys of birds, amphibians and fish using field observations and eDNA metabarcoding. I have related various habitat characteristics at the local and landscape scales to obtain estimates of i) the number of breeding bird pairs, ii) the number of chicks, iii) occurrences of amphibian species and iv) occurrences of fish species. Additionally, I investigated whether fish, amphibian, and bird communities could co-exist so that we could create wetlands to promote not only one, but multiple taxonomic groups. Thus, I explored the breeding bird community and their reproductive success in 89 constructed biodiversity wetlands and wetland use by fish and amphibian species in a subset of 52 created wetlands.

I found that wetlands created for biodiversity provided habitat for more than 80% of birds, 50% of fish and all amphibian species in the Uppland region. While wetland birds were related to larger wetlands, fish and amphibians did not prefer a certain wetland size. I also found that several small created wetlands could benefit adult birds similarly to a single large wetland. In fact, several small wetlands could accommodate more chicks than a single large wetland. Reeds, cattail, lilies, duckweed and other water vegetation, was an indicator for a high amphibian but low bird diversity. Wetlands with a higher proportion of flooded wet meadow areas in the wetland surroundings were bird-rich, but wetlands surrounded by shrubs and trees were less good in terms of bird diversity. However, the bird chicks were not so common in wetlands surrounded by a considerable amount of forest, as was the case for fish species. Fish were seen more often in wetlands that are connected to other wetlands, while amphibians were more likely to be found in isolated wetlands. When it comes to bird-fish-amphibian synergies and conflicts when creating wetlands for general biodiversity, it seems that fish might play a negative role in wetland occupancy by amphibians and possibly by birds. On the other hand, clear positive bird-amphibian associations could indicate that birds and amphibians would share created wetlands simultaneously without much trouble.

It seems that wetland restorations benefit at least half of the bird communities that are known to use wetland habitats. However, some population decreases following the restoration were also revealed in these studies. The analyses of the wetland restorations for birds indicated that the populations of gulls and terns increased considerably following restorations. The degree of increase varied markedly, but on average, the observed outcome could be somewhere between 56% and 325%. Grebes and diving ducks (19% and 153%), swans and dabbling ducks (2% decline and 102% increase), geese and smaller waders (between 6% and 92%) have all increased in their numbers following the restoration. On the other hand, the outcome for larger waders, rallids, warblers, raptors and owls was variable. The success being as high as 52% and failure as low as 58%. Unfortunately, after the restoration was executed, a clear population decline was between 11% to 59% for songbirds and finches. As there was high variability in the results for species and wetlands, and because many wetlands do not have appropriate surveys, it is difficult to know for a specific wetland and species if the effort/money has been worth it.

In this thesis, I have pinpointed which habitat requirements are more likely to benefit breeding birds and their young, amphibians and occasionally fish. I have also hinted that multiple small wetland creations could be just as beneficial as the creation of fewer large ones for birds. Furthermore, I showed that wetland creation synergies might be achieved in the future, especially for amphibian and bird communities. However, differences in habitat preferences and species co-occurrence mean that conservation conflicts could arise between fish and birds, as well as fish and amphibians. By studying several taxonomic groups and employing a range of analytical methods on pre-existing observations and targeted survey data, this thesis can help to improve a more cost-effective future wetland creation for biodiversity and inform future research directions, such as testing environmental and species interactions. I also showed how much wetland restorations contribute to the local bird population growth at the national level, which can inform restoration efficiency, help set clear biodiversity goals and improve future restoration efficiency. Finally, I expressed the need for environmental protection agencies and other funding bodies to promote standardised before-after wetland restoration surveys of birds. Such survey designs could lead to more illuminating restoration evaluations, making the improvement of wetland restorations also more cost-effective.

Populärvetenskaplig sammanfattning

Våtmarker är ett av de viktigaste ekosystemen för människor, vilda djur och växter. De bidrar med mat, utgör habitat för en rik biologisk mångfald, skyddar mot översvämningar, bidrar till att hantera klimatförändringar, samt är fantastiska platser att tillbringa sin fritid vid. Under de senaste hundra åren har många våtmarker dikats ur för att gynna jordbruk, gruvdrift, och skogsbruk, eller så har de exploaterats eller förorenats i urbaniseringens spår. Som en konsekvens av detta har många våtmarker försvunnit eller degraderats så att de inte längre utgör fungerande ekosystem. Som en konsekvens av detta, har många djurarter som nyttjar våtmarker, vilka i min avhandling var fåglar, amfibier och fiskar, visat sig inte må så bra under de senaste årtiondena, det vill säga de har minskat eller försvunnit. Men dessa tre djurgrupper är essentiella för bibehållandet av levande och blomstrande våtmarksekosystem. Därför har naturvårdsinsatser gjorts för fåglar och groddjur och, i mindre utsträckning, fiskar, insatser som kan sammanfattas som restaureringar av degraderade våtmarker samt skapandet av helt nya våtmarker. Dessa åtgärder började för 30-40 år sedan och har blomstrat till ett tydligt stöd för våtmarksarter idag.

Trots detta finns det flera saker vi inte vet när det kommer till att skapa och restaurera våtmarker för att öka mångfalden av djur. Vi saknar storskaliga studier om vad som händer med djurlivet efter skapandet eller restaureringen, där man undersöker flera olika våtmarker samt djurgrupper. För att fylla denna kunskapslucka undersökte jag effekten av restaureringar av 37 olika våtmarker i svenska jordbrukslandskapet på olika våtmarksfåglar genom att jämföra antalet häckande på före respektive efter restaureringen. För att kunna beräkna effekten av våtmarksrestaurering tog jag hänsyn till nationella bakgrundstrender i de olika arternas nationella populationer. Då dessaa data inte var insamlade med samma metodik, använde jag metaanalys.

Även om vi redan vet mycket, så vet vi inte hur fisk, fåglar och groddjur lever i våtmarker skapade för biodiversitetsändamål. Det är tänkbart att nyskapade våtmarker inte kan upprätthålla samma mångfald som naturliga våtmarker, men vi kan fortfarande lära oss och utveckla anläggandet och konstruerandet av våtmarker för att uppnå så hög nivå av biologisk mångfald som möjligt. En viktig komponent som ofta inte undersöks är vilka egenskaper hos våtmarker som gynnar produktionen av ungar. Därför har jag jämfört olika habitategenskaper på lokal- och landskapsnivå med i) antalet häckande fågelpar, ii) antalet fågelungar, iii) förekomst av groddjur samt iv) förekomst av fisk. Utöver detta har jag undersökt huruvida fisk-, groddjur- och fågelsamhällen kan samexistera så att våtmarker kan skapas för att gynna flera djurgrupper samtidigt. Jag undersökte häckande fåglar samt deras reproduktiva framgång i 89 skapade våtmarker, samt förekomster av fiskar och groddjur med hjälp av DNA fragment i 52 av dessa våtmarker. Vad har jag då funnit?

Jag fann att våtmarker skapade för biologisk mångfald utgjorde habitat för mer än 80% av fågelarterna, samt 50% av fiskarterna och alla arter av groddjur i vårt undersökningsområde i Uppland. Våtmarksfåglar var kopplade till större våtmarker, men ingen tydlig sådan koppling hittades för förekomst av fiskar och groddjur. Jag fann också att flera mindre våtmarker gynnade adulta fåglar på liknande sätt som ett stort gjorde, men att produktionen av fågelungar var högre när man jämförde flera mindre våtmarker mot skapandet av en stor. Vass, kaveldun, svärdsliljor, nate och annan vattenvegetation var en indikator för hög artrikedom av groddjur, men en låg rikedom av våtmarksfåglar. Våtmarker med en högre andel översvämmad ängsmark i omgivningen var fågelrika, men våtmarker omgivna av busk- och trädmark var det inte. Fiskar fanns oftare i våtmarker med högre grad av konnektivitet via vattendrag och diken, medan groddjur förekom mer i isolerade våtmarker. Både produktionen av fågelungar och antalet fiskarter var negativt relaterad till skog i näromgivningen. När det kommer till synergier och konflikter mellan fåglar, fiskar och groddjur vid skapande av våtmarker för mångfald så tycks det som att fiskar kanske spelar en negativ roll för förekomst av groddjur och fåglar men att fåglar och groddjur är positivt associerade.

Hur bra fungerar jordbrukslandskapets våtmarksrestaureringar på fågelfaunan då? Det tycks som att våtmarksrestaurering gynnar åtminstone hälften av fågelarterna som är kopplade till våtmarker. Men, några populationsminskningar efter restaurering påvisades också. Analyserna indikerade att populationer av måsar och tärnor ökade efter restaurering. Graden av ökning var osäker, men skattningarna tyder på att den genomsnittliga ökningen låg någonstans mellan 56% och 325%. Doppingar och dykänder ökade med mellan 19% och 153%, gäss och mindre vadare med mellan 6% och 92%, medan svanar och simänder hade en förändring på mellan en minskning på 2% och en ökning på 102% efter restaurering. Däremot var utfallet för större vadare, rallar, sångare, rovfåglar och ugglar ännu mer variabel. Ökningen var i vissa fall så hög som 52% och minskningen i andra så stor som -58%. Den fågelgrupp som klart missgynnades av våtmarksrestaureringar var typiska buskhäckande arter som flera sångare – de minskade med mellan 11% och 59%. Slutligen, även om stora resurser investerats för restaurering så fann jag att många våtmarker saknade undersökningar av fågellivet för att utvärdera hur väl restaureringen lyckats och framför allt saknades före-efter undersökningar under flera år.

I min avhandling har jag pekat ut vilka miljökrav som är viktiga för häckande fåglar, deras ungar, groddjur samt, ibland, fiskar i anlagda våtmarker. Jag visar att flera små våtmarker eventuellt kan ha samma eller bättre effekt för att gynna fågellivet som en motsvarande stor våtmarker. Utöver detta visar jag att våtmarker kan skapas så att de samtidigt gynnar groddjur och fåglar. Men, naturvårdskonflikter kan uppstå mellan fiskar och fåglar-groddjur eftersom det kan finnas negativa kopplingar orsakade av fiskar som konkurrenter och predatorer i dessa ofta små och begränsade vatten. Därför kan min avhandling hjälpa till att uppnå mer kostnadseffektivt nyskapande av våtmarker för mångfald och vara en kunskapskälla för framtida forskning för att t. ex. testa miljö- och artinteraktioner. Jag visade också hur mycket våtmarksrestaureringar tillför lokala fågelpopulationer, något som kan hjälpa till att sätta tydliga mångfaldsmål samt öka framtida restaureringseffektivitet. Till sist påvisade jag nödvändigheten av att organisationer som spenderar resurser på restaureringar av våtmarker utför standardiserade före-efter utvärderingar, vilket på sikt kan göra förbättringen av våtmarksrestaureringar mer kostnadseffektiv.

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Policy analysis

Evaluating created wetlands for bird diversity and reproductive success

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ABSTRACT

Wetland creation is a common conservation practice to mitigate biodiversity loss, caused by global wetland destruction. Despite this, there is a lack of large-scale evaluations of how created wetland characteristics and landscape context relate to bird diversity and reproductive success. We inventoried 89 created wetlands (0.2–20 ha) in central Sweden to investigate which local and landscape components were associated with breeding wetland bird species richness, pair abundance and reproductive success. Wetland size was positively associated with species richness, pair abundance and chick abundance. However, several small (1 ha) wetlands taken together were similar to or exceeded individual large wetlands of similar total wetland area, in terms of species richness, pair abundance, and chicks produced. While species richness showed a clear negative relationship with the proportion of the adjacent 50 m buffer composed of forest, pair abundance was positively related to the proportion of flooded grassland area and negatively related to the proportion of emergent water vegetation. Reproductive success measures showed no clear relationships to local habitat characteristics but tended to increase with a decreasing forest at the landscape scale. Our results suggest that breeding wetland bird populations could benefit from creating wetlands with a high flooded area, continuous management to minimise both the area of emergent water vegetation and the establishment of shrubs and trees in the immediate surroundings. We also suggest a practice of creating mainly small wetlands with a few larger ones to facilitate breeding wetland bird communities at the regional scale (gamma diversity).

1. Introduction

Wetlands are important ecosystems providing multiple ecosystem services, such as nutrient retention, water quality improvement, carbon storage, protection from flooding, food provision and recreational values (Maltby and Acreman, 2011; Zedler and Kercher, 2005). However, since the beginning of the 20th century, as many as 60–70% of all wetlands worldwide have been lost due to agricultural drainage and urbanisation (Davidson, 2014), and of those remaining, many are degraded (Zedler and Kercher, 2005). Consequently, it is suggested that the decline of wetland biodiversity is greater than that in terrestrial systems (Dudgeon et al., 2006; Millennium Ecosystem Assessment, 2005). Among avian wetland species, about 55% are declining worldwide, although large herbivorous waterbirds are increasing (BirdLife International, 2017; Wilson et al., 2005; Montràs-Janer et al., 2019; Pöysä et al., 2019). Many conservation measures to abate wetland biodiversity declines have been implemented, including wetland protection (e.g. Ramsar convention), restorations and creations (e.g. agri-environmental schemes).

Created wetlands can be efficient in promoting diversity of water plants and insects similar to that in natural wetlands (Balcombe et al., 2005; Bantilan-Smith et al., 2009; Desrochers et al., 2008; Hartzell et al., 2007). They are relatively poor, however, in promoting breeding bird community diversity relative to natural wetlands (Desrochers et al., 2008; Sebastián-González and Green, 2016; Snell-Rood and Cristol, 2003). Thus, several questions can be raised when creating wetlands for bird conservation. How can we improve breeding bird diversity when constructing wetlands for biodiversity? Are the size (cf. Sebastián-González and Green, 2016), certain constructed habitat elements and the landscape context important for attracting wetland species? How do

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these characteristics relate to reproduction?

Several studies have evaluated the relationship between environmental variables and wetland birds within created wetlands in agricultural landscapes (Choi et al., 2015; Froneman et al., 2001; Sánchez-Zapata et al., 2005; Sebastián-González et al., 2010). However, in most studies wetlands were created for other purposes than biodiversity, including rice fields, irrigation or nutrient retention ponds, and abandoned quarries (McKinstry and Anderson, 2002; Sánchez-Zapata et al., 2005; Strand and Weisner, 2013; Tourenq et al., 2001). Large-scale studies on wetlands specifically created to facilitate wetland biodiversity are lacking. Furthermore, most studies on created wetlands investigate relationships between environmental variables and species richness and abundance. The effects on reproductive success are rarely evaluated (but see McKinstry and Anderson, 2002) and the chicks may have different needs than adult birds (Nummi and Pöysä, 1993). As with many other human-modified habitats (Battin, 2004), created wetlands may attract birds to breed but provide poor breeding conditions, due to increased predation, for example, thus functioning as ecological traps (cf. Desrochers et al., 2008). Furthermore, the landscape context may affect bird communities in created wetlands (Li et al., 2019; Pérez-García et al., 2014), but little is known about this, especially so in biodiversity wetlands. We do know that landscape composition can affect nutrient supply and predator communities, causing food availability and predation rates to vary among landscape types (Lehikoinen et al., 2016; Padyšáková et al., 2011; Pavón-Jordán et al., 2017). We need to consider the landscape in addition to local habitat attributes when evaluating the effects of created wetlands on wetland bird diversity and reproductive success.

Conservation strategies of creating new habitats should also consider whether it is more beneficial to create single large or several small (SLOSS) habitat patches of the same total area, as the creation of small wetlands may be cheaper and more practical to create but less beneficial for bird species preferring large wetlands. Historically, SLOSS comparison focused on what habitat size should be prioritised for biodiversity protection, often using species richness as the primary evaluation metric (Diamond, 1975; Simberloff and Abele, 1976). Recent evidence indicates that several small habitat patches together contribute similarly or more to species richness than a single large habitat patch of the same surface area (e.g. Deane et al., 2020; Fahrig, 2020). However, the SLOSS debate regarding habitat creation or involving other diversity measures, such as abundance, has not been thoroughly previously investigated. As any conservation strategy goals ultimately also involve an increase in biodiversity productivity, one should also consider the SLOSS creation strategy regarding reproductive success.

In Sweden, considerable funds have been invested in wetland creation and restoration to reach the national environmental goal of “Thriving wetlands” (Svensson, 2015). Since 1989 more than 1000 smaller wetlands (usually <5 ha in size) have been created, the majority to facilitate wetland biodiversity (SEPA, 2019, 2009). Our research aims to investigate the knowledge gaps concerning the successful creation of wetlands for higher diversity and reproductive success of wetland birds. First, we investigated how local habitat characteristics of the created wetlands relate to wetland bird diversity (species richness and pair abundance) as well as reproductive success. Second, we examined how landscape context affects these diversity measures. Last, we investigated whether single large or several small created wetlands support more wetland bird species, higher total pair abundance and, ultimately, greater reproductive output.

2. Materials and methods

2.1. Study area

In the province of Uppland (Fig. 1), Sweden, the majority of 170 known created wetlands have been constructed to improve wetland bird diversity (Dietrichson, 2017). Most of the created wetlands in this area consist of wetlands created in terrestrial sites. However, in some instances, wetlands were created at sites that had a wetland drained and converted into arable land or conventional forest at some point in history (>50 years before, wetland recreation). This region’s landscape consists of a mosaic of managed boreal forest and agricultural land, with more forest in the northeast and more agricultural land in the southwest. During the last 150 years, the forests and arable land have been drained, reducing the amount and area of existing natural wetlands (Fredriksson and Tjernberg, 1996). Still, it is a region with many natural wetlands and lakes of which most are oligotrophic and situated in coniferous forest.

We performed a stratified random wetland selection in order to keep a similar variation of local habitat characteristics (size, number of

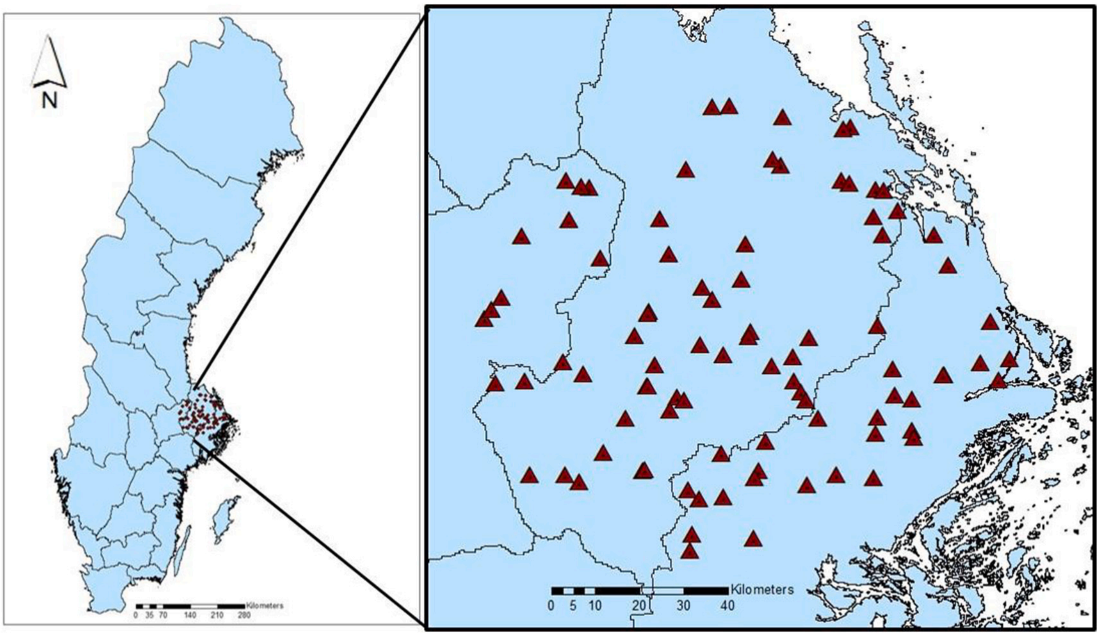

Fig. 1. The 89 surveyed created wetlands located in Uppland region (including Uppsala, and parts of Västmanland and Stockholm counties; 59°51′29″N 17°38′41″E).

separate open water bodies (ponds) within a wetland, the proximate area with forest, see Section 2.2 and Table 1) in different landscape types (forest- or agriculture-dominated: >50% and < 50% of forest respectively within 1 km buffer). Each habitat characteristic was thus equally distributed over environmental gradients. The 89 selected wetlands (Fig. 1) ranged in size between 0.14 and 20 ha; 70 wetlands were located in forest-dominated and 19 in agriculture- dominated landscapes. Most wetlands were created as single water bodies, but in 22 cases, multiple separate ponds (i.e. wetland complex) located next to each other were constructed. The wetlands also varied in depth, shape, shore steepness (though related to flooded area) and connectivity to watercourses, but these characteristics were not measured. Some wetlands have been managed by occasionally removing shrubs and aquatic plants (e.g. reed, cattail, floating vegetation), by grazing or mowing adjacent grassland, or by supplementary feeding of birds and introduced mallard chicks.

2.2. Habitat and landscape context

We collected data on local and landscape-scale characteristics known or hypothesised to affect bird diversity and reproductive success (see Appendix A1). We used ArcGIS software (v. 10.5), recent aerial photographs (2015/2017, Lantmäteriet), field notes, Swedish terrain and human population density maps (GSD Geografiska Sverigedata; Statistiska centralbyrån 2019) to estimate the area of: i) wetland surface, ii) water vegetation, iii) wooded and open islands, and within 50 m buffer from the wetland shore, iv) trees/bushes, and v) flooded grassland, as well as a count of vi) the number of ponds (see Table 1 for definitions). We also determined the presence of inflow (mainly preventing the wetland from drying out) and, within a 1 km buffer, the cover of urban area and forest (Table 1). We hypothesised that coniferous forest within the landscape could affect predator communities (Elmberg and Gunnarsson, 2007) and water quality, via acidity and lower nutrient levels than agriculture-dominated landscapes (Lehikoinen et al., 2016). The proportion of urban areas can be expected to positively and negatively affect bird communities in created wetlands. Humans may supply food and repel predators (for instance, settlements may repel mink predations, Brzeziński et al., 2012), but also increase disturbance and support a higher density of domestic predators. Last, we calculated the water area of neighbouring wetlands within a 3 km buffer because we expected bird communities in created wetlands to be influenced by dispersal and meta-community dynamics, affecting local species pool positively for some species but negatively for others (reviewed by Holopainen et al., 2015). We did not use spatial scales >3 km to avoid overlap between the sites at the landscape scale.

2.3. Bird surveys and response variables

Four standardised wetland bird inventories of the 89 created biodiversity wetlands took place during the breeding season in 2018: twice during the period when birds were settling or started breeding (14–29 May, "settlement stage"), and twice during the chick-rearing period (18 June–3 July, "reproductive stage"). The timing of the settlement stage was chosen to cover both early and late breeding species, and this is the same time period as used by the wetland bird national inventory of Sweden (Green et al., 2020). For detailed methods of the surveys, see Supporting information Appendix A2 and Table A1.

During the settlement stage, the two first visits were used to estimate species richness (hereafter ***richness***) and the number of pairs (***pair abundance***) of each breeding wetland bird species at each site. For each species, we used the maximum pair abundance (including zeroes; see Table A1 for more details of pair estimates) out of two inventories.

To determine wetland suitability for breeding wetland birds and whether created wetlands contribute to their community growth, we estimated reproductive success of a subset of 21 species for which chicks were relatively easy to detect (mainly ducks and grebes; Table A2). First, ***chick abundance*** was the highest number of chicks seen in a wetland for each species (including zeroes for species with no chicks observed). Second, ***breeding success*** was determined for each species that was observed in at least one of the first two visits, with success denoted for species that were also observed with at least one chick during the visits. This measurement was used to reflect the reproductive success of each species. Chick abundance was used to reflect wetland productivity.

2.4. Statistical analyses

2.4.1. Testing bird community associations with the environment at local and landscape scales

We used generalised linear models (GLM, GLMM when using mixed-

Table 1
Environmental variables considered having a potential influence on the wetland bird community. The variables were estimated by using the digitalised field and land use maps. Mean, standard deviations and range are presented for 89 wetlands. The *italic* variable names indicate landscape-scale variables.

Variable	Scale	Definitions	Mean ± SD (range)
Size	Local	Water surface, including emergent water vegetation (ha)	3.37 ± 3.60 (0.14–19.98)
Water vegetation	Local	Water surface covered by one or more species of emergent water vegetation (e.g. *Typha*, *Phragmites*, *Iris*, etc.) (%)	26.82 ± 23.47 (0–100)
Open islands	Local	Area of constructed islands covered by grass vegetation or bare soil (ha)	0.08 ± 0.18 (0.00–1.48)
Wooded islands	Local	Area of constructed islands that were covered with bushes and trees (ha)	0.06 ± 0.10 (0.00–0.55)
Number of ponds	Local	Number of separate created water bodies (pools) in a wetland complex	1.66 ± 1.57 (1–10)
Flooded area	Local	Adjacent grassland that can be flooded (%), defined by soil humidity and wet grassland vegetation (50 m buffer surrounding the water surface shore)	7.87 ± 10.90 (0.00–54.79)
Local forest	Local	Adjacent area with trees and bushes (%) (50 m buffer surrounding the water surface shore)	51.66 ± 29.96 (0.00–99.99)
Management	Local	Presence (yes/no) of management (grazing, mowing, shrub removal, feeding stations, water vegetation management, within wetland and 50 m buffer).	25 managed/ 74 non-managed
Year	–	Year wetland was created. When this was not known, the year interval (max five years) was assigned based on aerial photos, and the maximum year was used as an entry	2001 ± 6 (1985–2017)
Inflow	Local/ Landscape	Whether wetland is hydrologically connected (yes/no) providing water influx (ditches, streams, water pumps (latter just 2 cases)), so that water levels are less dependent on rain	38 with/ 51 without
Landscape forest	Landscape	Forest area within 1 km buffer (%) outside and extending from the 50 m buffer surrounding the shore (when the forest is <50%, the landscape is open)	63.97 ± 23.19 (0.96–100)
Urban area	Landscape	Area with at least one registered person living (100 m^2 resolution) within 1 km buffer extending from the 50 m buffer surrounding the shore (%)	4.76 ± 6.80 (0–50.94)
Neighbouring wetlands	Landscape	Area of water bodies within 3 km buffer extending from the 50 m buffer surrounding the shore (%)	4.13 ± 8.33 (0–65.43)

effects) to evaluate the relative importance of the environmental variables at local and landscape scales on two groups of response variables: two indices for bird diversity (***richness*** and ***pair abundance*** during the settlement stage), and two indices of reproductive success (***chick abundance*** and ***breeding success*** during the reproductive stage), resulting in four models in total. The models included 13 explanatory environmental variables listed in Table 1.

We modelled ***richness*** using GLM with a Poisson error distribution ($n = 89$). For ***pair abundance***, we used GLMM with negative binomial error distribution due to over-dispersion. This model contained species and wetland identities as random effects that account for different population sizes across wetlands and species. An alternative would have been to use total abundances summed over all species; however, this would result in estimates heavily driven by the most common species. Pair abundance of each species at each wetland was a single data record ($n = 3382$), including zeroes at each site where a species was not observed.

Chick abundance was modelled similarly to pair abundance using GLMM with negative binomial error distribution and species and wetland identity as random effects ($n = 462$). We included zeroes only at sites where we observed adults at the settlement stage for a species but not chicks in the reproductive stage. We included logged pair abundance from the settlement stage as an explanatory variable to account for the higher chick abundance at sites with more pairs. ***Breeding success*** was modelled using binomial GLMM, with species with chicks identified as successful and species observed as adults but without chicks as a failure ($n = 434$). The breeding success GLMM also used species and wetland identities as random effects and included logged pair abundance as an additional explanatory variable.

All explanatory variables were centred and scaled to make the coefficient estimates directly comparable. Due to data distribution heterogeneity, wetland size was logged, and both areas of wooded and open island variables were square-root transformed before scaling. We used a full model approach as we were interested in estimating and showing the effects of all variables expected to be biologically relevant (Table 1). We only removed variables due to multicollinearity. Multicollinearity among explanatory variables was evaluated using the variance inflation factor (vif), where variables with vif values >4 were removed. For a comparison to our full model approach, we also performed model averaging (MuMIn package, Bartoń, 2020) for all four responses to calculate the importance of each variable included (see Supporting Information Table A3). All analyses were done in R 3.6 (R Core Team, 2019), using package glmmTMB (Brooks et al., 2017) for all GLMMs.

2.4.2. SLOSS wetlands

We also investigated the effects of wetland size at the regional scale. First, we looked at whether cumulative species ***richness*** differed between the cumulative wetland area when combining sites in a different order: from large to small and from small to large (Quinn and Harrison, 1988). Then, to estimate the potential cumulative contribution of small wetlands to the regional wetland pair and chick abundance, we used predictions, with their uncertainties, of wetland size from GLMMs described above. We estimated the expected total ***pair abundance*** and ***chick abundance*** (but pair abundance was not included in the latter GLMM inference) for different wetland sizes (1, 5, 10, 15, 20 ha) by multiplying the predictions (and standard errors) of wetland size from GLMM models to a total of 20 ha (corresponding to the largest wetland in our sample). For instance, 1 ha pair estimate with its standard error was multiplied by 20, a 5 ha estimate by 4, etc. To represent the community level predictions, we set the random effects (species and site identity) to zero so that the predictions obtained were for an averaged species and wetlands. The rest of the environmental variables were set to their means to single-out size effects.

3. Results

In total, we observed 38 breeding wetland bird species, 1521 pairs and 2024 chicks at the surveyed 89 created wetlands. The most common species were mallard *Anas platyrhynchos* (218 pairs), common coot *Fulica atra* (197) and common goldeneye *Bucephala clangula* (94), see Table A2 for details.

3.1. Local habitat

Both species richness and pair abundance were much higher in large than small created wetlands (Figs. 2a, 3a–b, Table A3), and wetland size explained considerably more variation than other environmental variables. Variation in richness and pair abundance showed similar associations with local wetland characteristics (Fig. 2a, Fig. A1, Table A3). Pair abundance was associated with several local habitat characteristics: positively with proportion of flooded area (Fig. 3c-d, Table A3) and negatively with the proportion of water vegetation (Fig. 3g). Additionally, species richness showed a clear negative association with local forest (Figs. 2a, 3f, Table A3). Neither richness nor pair abundance showed clear relationships with other local characteristics such as islands, the number of ponds within the wetland, water inflow or absence of management (but see the negative tendency for local forest Fig. 3e; and management Fig. 3h).

Reproductive success measures showed no clear relationships with local habitat characteristics (Figs. 2b, A2, Table A3) except for wetland size which positively associated with chick abundance (Fig. 4c). Reproductive success measures were explained mainly by pair abundance (Figs. 2b, 4a–b).

3.2. Landscape context

Richness and pair abundance were not distinctly related to surrounding landscape variables (Figs. 2a, A1, Table A3). Reproductive success was not clearly related to landscape context, although breeding success tended to associate negatively with the landscape forest (Fig. 4d, Table A3). Overall, the results between our full model and the model averaging are relatively similar; see Table A3 in supporting information for details of model averaging results.

3.3. SLOSS wetlands

Locally, larger wetlands hold more species than small wetlands. However, at the regional scale, the cumulative species richness of several small wetlands (e.g. <1 ha) was similar to that of a single large when representing the same accumulated wetland area as species accumulation curves overlap (Fig. 5). Although several small wetlands together had seven species more than the largest wetland (i.e. 20 ha), overall, the cumulative species richness of the smallest wetlands were similar to the large ones. Predicted pair abundance for multiple sites making up a total of 20 ha was also similar in several small compared to a large wetland, though the difference was 0.5 pair higher in smaller wetlands (Fig. 6a, that is for an average species in an average wetland, see Section 2.4.2). In contrast, predicted total chick abundance was distinctly higher (~25 chicks) for several small compared to single large created wetlands when comparing the same created area (Fig. 6b, that is, for average species in an average wetland, see also Fig. A3c).

4. Discussion

Many countries are experiencing vast wetland destruction (Davidson, 2014) and new wetland creation to mitigate habitat loss is accelerating (Niu et al., 2012). Our results suggest how to improve wetland creation for wetland birds in the Northern hemisphere and highlight the importance of including measures of reproductive success and a landscape perspective in wetland creation evaluations. Richness and pair abundance were associated with several local characteristics (e.g. proportion of flooded area, local forest and water vegetation), whereas we found no distinct relationship with surrounding landscape characteristics. In contrast, variation in reproductive success showed fewer

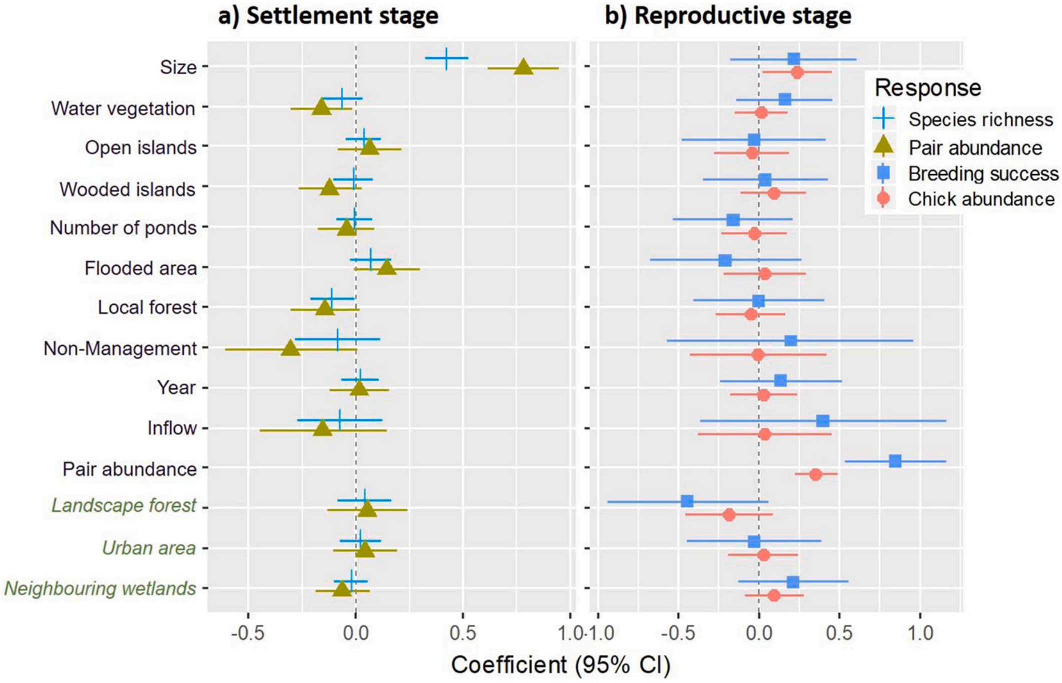

Fig. 2. Model coefficients and confidence intervals from models explaining variation in a) species richness and pair abundance, b) breeding success and chick abundance across 89 created wetlands of 38 species (21 for reproductive success). The coefficients are directly comparable (all predictors were centred and scaled; size and pair abundance were also log- and islands square-root-transformed). Predictors not considered have no estimates (see Table 1 for descriptions of environmental variables). Green italic variable names indicate landscape-scale variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

associations with local characteristics but tended to associate with the landscape context (e.g. forest at the landscape scale). We detected a strong positive effect of wetland size on local richness, pair and chick abundances, but no effect on breeding success measure. Still, several small wetlands can have similar breeding bird diversity and higher chick abundance as a single large wetland at a regional scale.

4.1. *Local habitat*

The positive relationships between richness and pair abundance with wetland area are in line with island biogeography theory and with previous findings on bird diversity in created wetlands (Froneman et al., 2001; Sánchez-Zapata et al., 2005; Sebastián-González et al., 2010; Sebastián-González and Green, 2014; Strand and Weisner, 2013). Wetland size was also related to chick abundance, but not with breeding success when pair abundance was included in the model. Very few studies have related wetland bird reproduction to the size of created wetlands (but see McKinstry and Anderson, 2002), but in natural systems, the size-reproductive success relationship is species-dependent (review by Holopainen et al., 2015). Any measure to improve wetland biodiversity should also aim to facilitate wetland bird reproductive success, but we often lack such information.

Our findings, as well as previous studies including natural wetlands, suggest flooded areas to be important when creating wetlands as they provide suitable foraging habitat, especially for waders and ducks (Milsom et al., 2002; Smart et al., 2006; Żmihorski et al., 2016). Flooded areas could also indicate the wetland's general shallowness, which benefits non-diving wetland species, but puts diving species at a possible disadvantage (reviewed by Ma et al., 2010). Additionally, high wetland bird abundance in flooded wetlands might be due to increased wetland productivity and habitat heterogeneity, which is especially important for wetlands within the boreal forest (where water conditions are usually oligotrophic, Nummi and Holopainen, 2014).

Prior research suggested that cover of emergent water vegetation benefits several breeding wetland bird species (Ma et al., 2010; McKinstry and Anderson, 2002; Sebastián-González et al., 2010), but our results contradict these findings (see Fig. 3g). The negative effects of water vegetation may reflect a decreased detection probability, as water vegetation may obscure visibility. It may also decrease the amount of foraging habitat for dabbling and diving birds (e.g. many duck species, grebes; reviewed by Ma et al., 2010). On the other hand, emergent water vegetation can offer good foraging and nesting opportunities as well as protection from predators for some species (Froneman et al., 2001; McKinstry and Anderson, 2002; Sebastián-González et al., 2010). The effects of water vegetation on the attraction of wetland birds are complex and likely differ between bird species and foraging guilds. Based on the knowledge from natural lakes in boreal forests, it seems to depend more on structural complexity than the coverage (Holopainen et al., 2015).

Additionally, species richness was also negatively related to the proportion of local forest. The negative relationship could be attributed to that trees and shrubs provide perching spots for avian predators, such as corvids (Holopainen et al., 2015), thus reducing the potential for high reproductive success and could therefore be avoided by some birds (Berg et al., 1992; Wallander et al., 2006). However, it could also be related to that bordering forest could reduce water nutrient levels (Licht, 1992), and thus the food availability.

It has been suggested that open islands may be important nesting habitats for several wetland bird species, including gulls, terns and ducks (Väänänen et al., 2016). Although some species were breeding on the islands, we found no distinct evidence for such effects of the whole wetland bird community on either settlement or reproductive stages. Reproductive success measures showed no simple relationships with local habitat characteristics except for chick abundance in relation to wetland size. The breeding pair density is one of the most important factors determining the higher chick abundance and breeding success of the wetland bird community in created wetlands.

The use of reproductive data is important when evaluating created

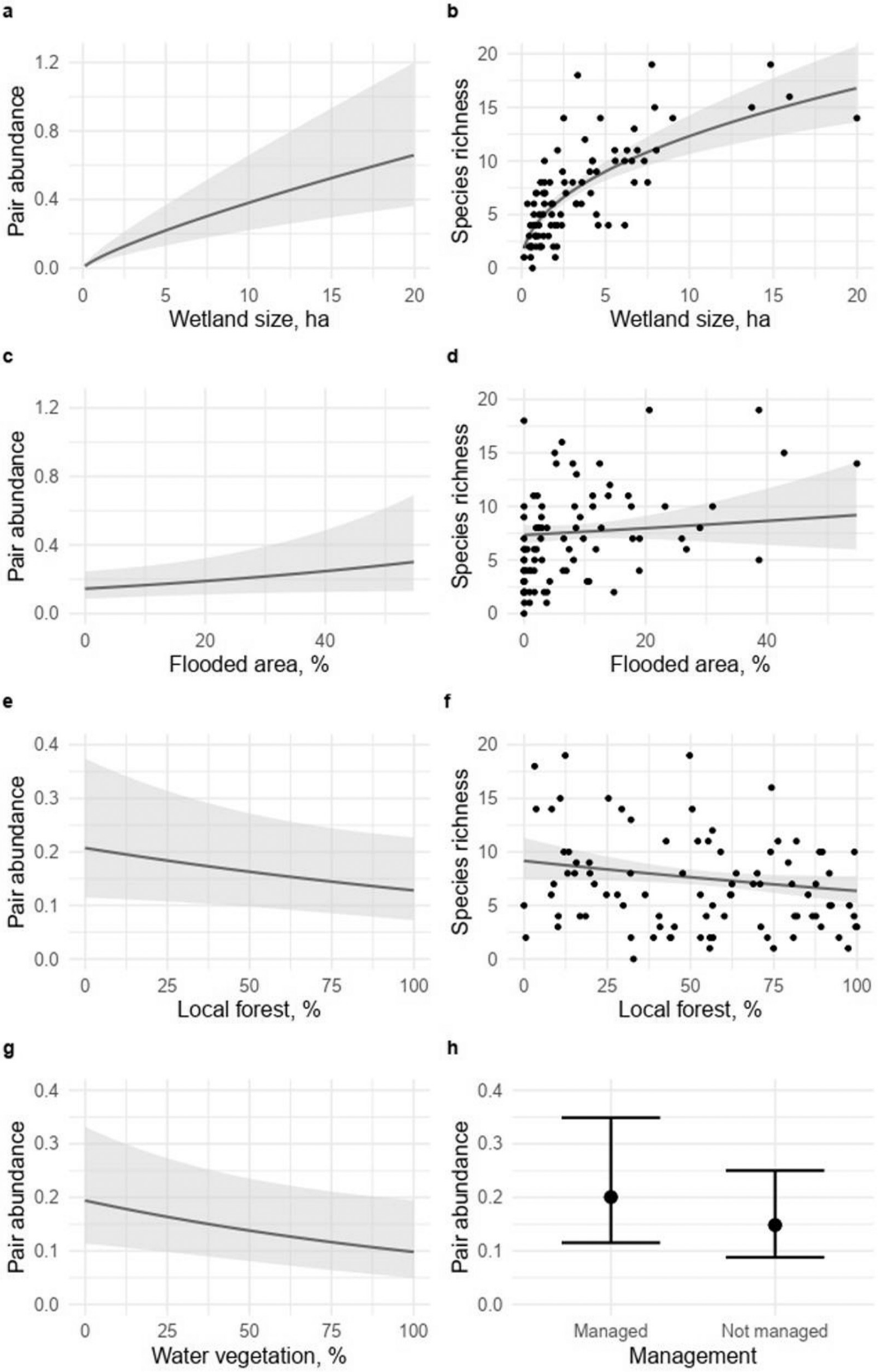

Fig. 3. Wetland bird species richness (right column, b, d, f) and pair abundance (a, c, e, g, h) in relation to selected characteristics of created wetlands as predicted by models summarised in Fig. 2a (shaded area shows 95% CIs). Black dots represent raw data points. The random effects (species and site identity) were set to zero, and the rest of the environmental variables were set to their means.

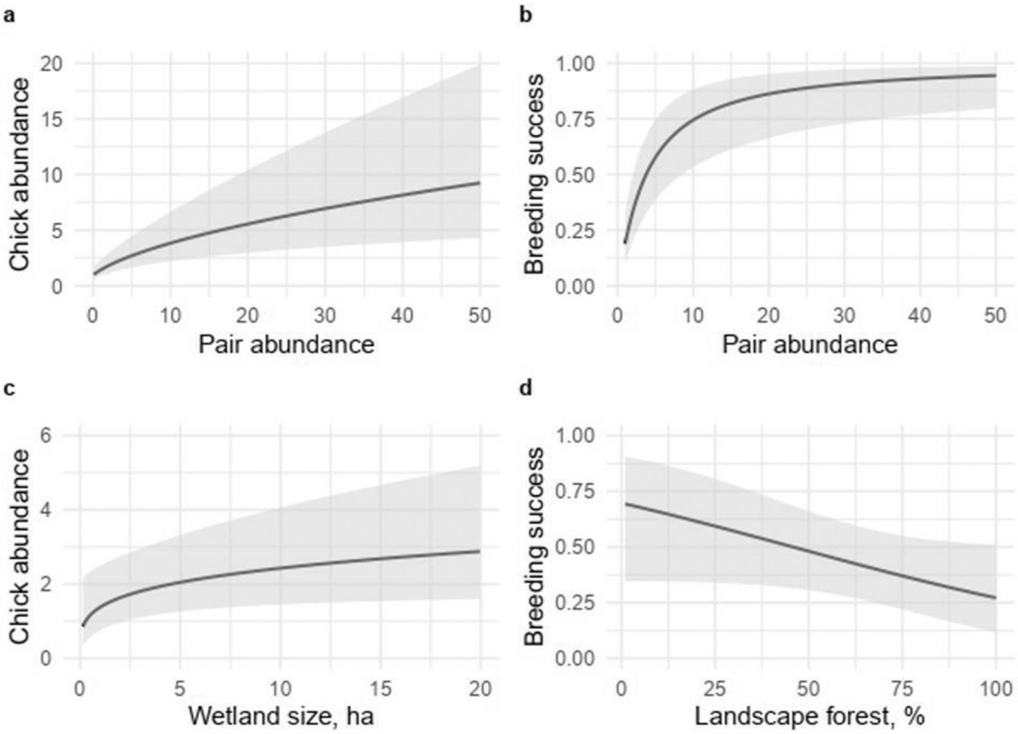

Fig. 4. Chick abundance (left column, a, c) and breeding success (right column, b, d) in relation to selected characteristics of created wetlands as predicted by models summarised in Fig. 2b (shaded area shows 95% CIs). The random effects (species and site identity) were set to zero, and the rest of the environmental variables were set to their means.

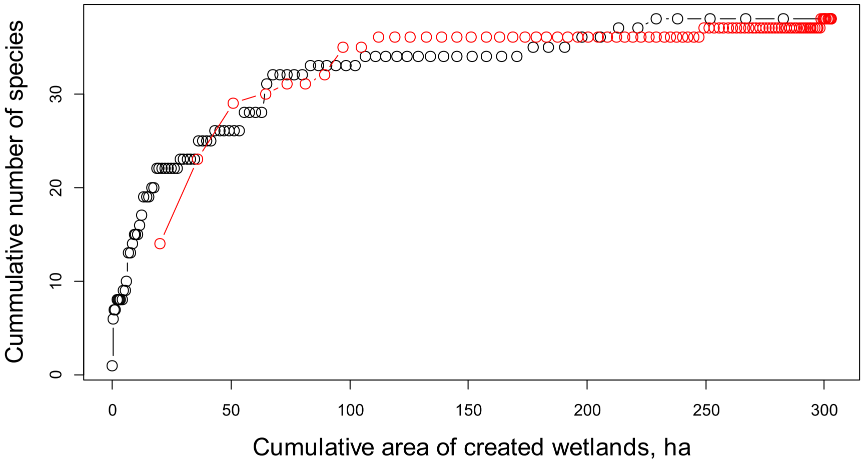

Fig. 5. Species accumulation plot (Quinn-Harrison curve) showing cumulative species richness as a function of cumulative area of created wetlands included. Black circles indicate accumulation direction from smallest to largest wetland, while red - from largest to smallest. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

wetlands, as high pair but low chick abundance could indicate an ecological trap mediated by human-modified habitats (Battin, 2004). Even though there were differences between the observed habitat-bird diversity relationships and habitat-reproductive success relationships, we did not find an indication that created wetlands might act as ecological traps. On the other hand, some species may move their chicks from the wetland of nesting to a wetland where the chicks are reared (e.g. goldeneyes, Paasivaara and Pöysä, 2008; even grebes Kloskowski and Frączek, 2017), thus adding some uncertainty to our estimates of local wetland bird diversity and reproductive success. However, wetlands with many broods and chicks should still represent high-quality wetlands for chick-rearing irrespective of the chick origin. Thus, chick movements do not change our general interpretations of what constitutes a good or bad wetland for reproductive success.

4.2. Landscape context

We found no distinct relationships between surrounding landscape characteristics and species richness or pair abundance at the settlement stage. This is surprising, as landscape context has been shown to relate with wetland birds in natural systems (Holopainen et al., 2015; Pavón-Jordán et al., 2017). Although the relationship between bird diversity and landscape context may vary between the spatial scales used, our general result of no clear relationship likely applies also at different

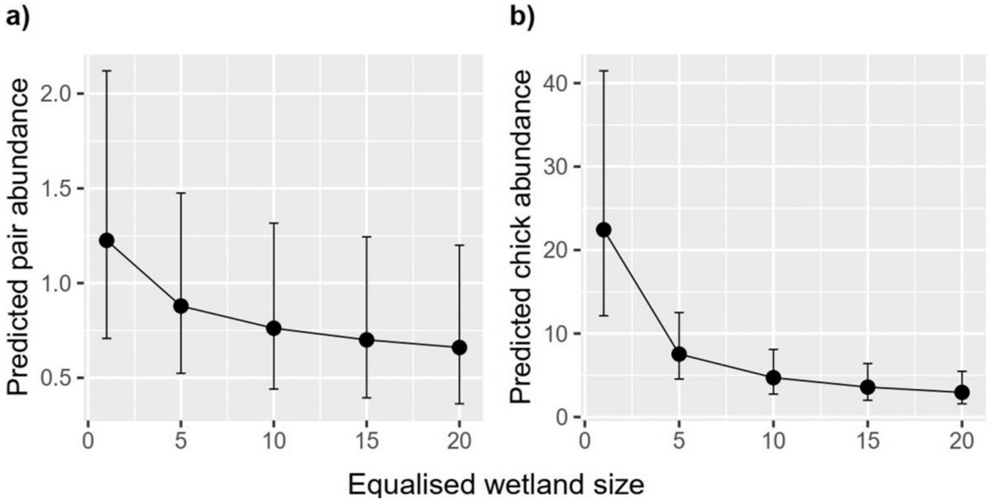

Fig. 6. Comparison of estimated effects of single large or several small wetlands on the abundance of pairs and chicks for multiple wetlands of different sizes, making up a total of 20 ha. The predicted pair (a) and (b) chick abundance when controlling for species and site identity and environmental variables (but not controlling for pair abundance in the analyses of chick abundance). Error bars refer to 95% confidence intervals.

spatial scales, as these are highly correlated ($r > 0.73$ for the three landscape types between one and three-kilometre buffers). However, landscape composition might be important for explaining reproductive success estimates. Though highly uncertain in our full models, and not statistically clear, the proportion of forest within the landscape showed the strongest support among the environmental variables, suggesting a possibly negative effect on reproductive success (see Fig. 2b). Predation pressure is unlikely to be higher in forest dominated landscapes (Holopainen et al., 2020). The most likely explanation, however, could be the lower food availability in oligotrophic wetlands (which are usually found in coniferous forest-dominated landscapes) than in eutrophic wetlands, which are generally located in agricultural landscapes (Holopainen et al., 2015; Pöysä et al., 2001). However, with this paper's analysis, we intended to explore what variables might affect breeding bird community and infer productivity in created wetlands. To establish more definitive evidence of ecological effects on such communities, further studies, preferably experiments, are required.

4.3. *SLOSS wetlands*

A recent review including 157 studies focusing on SLOSS comparisons showed that most studies suggest several small habitat patches support greater total species richness than single large patches (Fahrig, 2020; see also Deane et al., 2020). One reason for this pattern could be biased sampling, where a higher sampling effort per unit area is exerted in small than large habitat patches (Gavish et al., 2012). Nevertheless, the results of studies with unbiased sampling effort (75 studies) still showed more species in several small than a single large habitat patch (52% of studies) while the other studies were inconclusive (37%) or supported single large over several small (11% of studies, Fahrig, 2020). Our SLOSS comparisons were also based on unbiased sampling (i.e. with a similar sampling effort/ha; see Section 2.3 and Supporting information A2). Our species accumulation curves crossed each other (Fig. 5) thus suggesting inconclusive results concerning SLOSS comparison on species richness (sensu Fahrig, 2020). Thus, scenarios of single large or several small created wetlands of the same total area would likely produce similar gamma diversity between both scenarios.

In addition to species richness, we also compared abundance measures between SLOSS wetlands, a biodiversity indicator usually not tackled in previous SLOSS research. We estimated pair and chick abundances based on model predictions that were adjusted to match the same total created wetland area (20 ha). While there was no apparent difference concerning pair abundance, results on chick abundance suggested that the creation of several small wetlands (1 ha) would be better than a single large equalling the same total wetland area (Fig. 6). One potential reason for this pattern could be that small wetlands have a higher shore/area-ratio with relatively more shore habitats in small compared to large wetlands. This habitat structure benefits many dabbling ducks and waders (Eriksson, 1983; Nilsson, 1986). Though a single large wetland has higher wetland bird diversity, a strategy of creating several small wetlands instead of a single large one is supported for reproductive success (at the community level) at the regional scale. Here a practical issue also comes into play concerning the uptake of landowners. As small wetlands are cheaper, easier to create, and do not require as much land as large ones (e.g. 20 ha), the uptake of creating small wetlands is higher among most landowners (as seen in the sizes of created wetlands in our study area). Furthermore, several species are known to be more common in small as compared to natural large inland wetlands (e.g. little grebe *Tachybaptus ruficollis*, moorhen *Gallinula chloropus*, Ottosson et al., 2012), although other species show preferences for larger wetlands (Black-throated loon *Gavia arctica* or Great crested grebe *Podiceps cristatus,* e.g. piscivores Nilsson, 1986). Thus, to benefit the wetland bird community at a regional scale, creating a mixture between many small and few large wetlands would be a good solution.

4.4. *Conclusions*

As small as they are, most of the created wetlands contribute to the regional species pool, i.e. gamma diversity, and are valuable for wetland bird conservation. In this region, 87% of the 45 regularly breeding inland wetland species (excluding passerines; Ottosson et al., 2012) were observed at our sites and many bred successfully. Out of these, four species are in the European red list (Slavonian grebe *Podiceps auritus*, Pochard *Aythya ferina*, Northern lapwing *Vanellus vanellus,* and coot) and 14 are in decline (Table A2). Overall, our results are in line with the general recommendations (see Appendix A1) for wetland creation for birds, for instance, by constructing low shoreline (to increase the area flooded), managing water vegetation so that wetlands do not become fully covered and reducing the cover of adjacent shrubs/trees. The use of reproductive success measures enabled us to detect the potential importance of the landscape context (i.e. coniferous forest within the landscape tended to reduce reproductive success). Although further research on landscape context is needed for clear conclusions, we suggest that future wetland creations should consider avoiding the surrounding coniferous forest within the landscape as a precautionary strategy. Lastly, our SLOSS comparison showed that while a single large wetland exhibited similar species richness and pair abundance levels compared with several smaller, the total production of young remained higher in multiple smaller wetlands at the regional scale. When resources for creating wetlands are limited, we therefore recommend creating several predominantly small wetlands over fewer and larger ones, especially in landscapes where large natural wetlands are already available.

CRediT authorship contribution statement

Ineta Kačergytė: Conceptualization, Methodology, Software, Data curation, Formal analysis, Writing- Original draft preparation, Visualization, Investigation, Writing- Reviewing and Editing.

Tomas Pärt:. Conceptualization, Methodology, Investigation, Funding acquisition, Writing- Original draft preparation, Writing- Reviewing and Editing.

Debora Arlt: Conceptualization, Methodology, Writing- Reviewing and Editing.

Åke Berg: Conceptualization, Methodology, Investigation, Writing- Reviewing and Editing.

Michał Żmihorski: Conceptualization, Methodology, Software, Writing- Reviewing and Editing.

Jonas Knape: Methodology, Software, Writing- Reviewing and Editing, Writing- Reviewing and Editing.

Zuzanna M. Rosin: Investigation, Writing- Reviewing and Editing.

Data availability

The data used in our analysis are available in an online repository https://snd.gu.se/en/catalogue/study/2021-90.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109084.

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ORIGINAL ARTICLE

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Environmental DNA metabarcoding elucidates patterns of fish colonisation and co-occurrences with amphibians in temperate wetlands created for biodiversity

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Abstract

1. Wetlands are biodiversity hotspots that provide several essential ecosystem services. On a global scale, wetlands have greatly declined due to human activities. To counteract wetland loss, created wetlands are used as a conservation tool to facilitate biodiversity and provide habitats mainly for birds and amphibians. Fishes are likely to colonise the created wetlands and potentially affect the diversity and occurrence of amphibians. Still, species occurrence data for fish in created wetlands are largely lacking.
2. Using eDNA metabarcoding, we investigated occurrence and co-occurrence patterns of fish and amphibian communities in 52 wetlands (some of which are ponds) created to benefit mainly bird and amphibian communities in south-central Sweden.
3. Altogether, 17 fish and five amphibian species were detected in the created wetlands out of the 32 fish and six amphibian species found in the regional species pool. Amphibians were less common in wetlands physically connected to other wetlands. Connected wetlands were more fish-rich than isolated ones, suggesting potential fish avoidance. Additionally, the amphibian community occupied a narrower environmental niche compared to the fish community. Nevertheless, we observed only five statistically significant negative fish–amphibian species co-occurrences (out of 14 species considered).
4. Even though our results suggest amphibian avoidance/exclusion from the created biodiversity wetlands, they also show that fish and amphibians frequently co-exist. Increased habitat heterogeneity in terms of water vegetation, size, shape, and structure of the wetland could be possible factors enabling the co-existence of these two taxa.
5. With this study, we contribute to the general knowledge of fish occurrence patterns in created biodiversity wetlands. By comparing the frequencies of fish occurrence in natural and created wetlands, we have shown that there was some

mismatch in what is common in natural compared to created wetlands. This mismatch probably comes from species-specific habitat requirements, stocking, and differences in detectability when using eDNA metabarcoding (small species detected) versus conventional multi-mesh gill-net methods (small species missed). Therefore, our results obtained using eDNA metabarcoding can complement the pre-existing knowledge of amphibian and fish associations and increase our understanding of how to create wetlands to facilitate biodiversity of several taxa.

KEYWORDS
connectivity, constructed ponds, species interactions, stocking, water community

1 | INTRODUCTION

Wetlands are rich ecosystems that provide multiple ecosystem services making them irreplaceable for biodiversity and humans (Kusler, 2012). Nevertheless, natural wetland habitat has been reduced by around 70% worldwide, mainly due to agricultural drainage and other human activities (Davidson, 2014). To counteract this, there is an increase in the creation of new wetlands (Dixon et al., 2016). Many of these wetlands are created to improve wetland biodiversity as compensation for its previous decline due to loss and deterioration of natural biodiversity-rich wetlands; for example, 400 wetlands were created for amphibians in Estonia (Magnus & Rannap, 2019; SEPA, 2019). Wetland protection has worldwide become a high priority, supported by international agreements such as the Ramsar Convention and the International Convention of Biological Diversity (Bobbink et al., 2007).

Amphibians and birds are common focal taxa for the conservation of wetland biodiversity, and the colonisation of created wetlands by these taxa is relatively well-documented in the literature (e.g. Baker & Halliday, 1999; Kačergytė et al., 2021; Porej & Hetherington, 2005; Sebastián-González & Green, 2014; Semlitsch et al., 2015; Shulse et al., 2012). Amphibians in particular seem to benefit from the creation of small wetlands (Magnus & Rannap, 2019), as their occurrence and establishment may depend on hydrology (preferred shallow, standing water), eutrophication (avoid hyper-eutrophication), presence of aquatic vegetation, distance to other wetlands and absence of predatory fish (reviewed by Brown et al., 2012). However, created wetlands are often connected with surrounding waterways for water level regulation, enabling fish colonisation. The colonisation of fish in created wetlands is rather common but generally not systematically recorded (Kristensen et al., 2020; Langston & Kent, 1997; Zimmer et al., 2001), and therefore fish community composition in created wetlands is often unknown. The construction features of created wetlands (e.g. dams vs. connected wetlands) vary, and some can affect the degree of accessibility for colonisations (Beatty et al., 2009; Talley, 2000), where the degree of isolation may be a strong factor diversifying fish species composition (Tonn et al., 1990). Natural colonisation by fish also depends on the movement rates (e.g. how active the fish is) and their regional abundance (Albanese et al., 2009). Additionally, fish occurrence can be related to human activities due to both legal and illegal stocking (Spens & Ball, 2008; Talley, 2000). The colonisation and presence of fish in created wetlands are likely to affect other taxa either by being a food source (e.g. for birds and newts) or by competition and predation (Bouffard & Hanson, 1997; Elmberg et al., 2010; Kloskowski et al., 2010; Semlitsch et al., 2015). Indirect effects may also manifest through altered water quality, loss of macrophyte diversity and cover via foraging activity, and management practices associated with angling activity (e.g. Lemmens et al., 2013; O'Toole et al., 2009; Schilling et al., 2009).

Fish are reported to have negative impacts on the growth and prevalence of amphibian populations (Pope, 2008; Semlitsch et al., 2015; Shulse et al., 2012) as well as their behaviour (Winandy et al., 2015). Amphibian population declines are also related to habitat loss or deterioration, over-exploitation, climate change and diseases (Cohen et al., 2019; Meurling et al., 2020; Stuart et al., 2004) and therefore are of conservation interest when creating new aquatic habitats. Negative effects of fish on amphibians, especially focusing on prey–predator occurrences, are well documented in natural wetlands (Hartel et al., 2007) and created ponds (Semlitsch, 1987). However, created wetlands constructed for improving wetland biodiversity and including potential amphibian–fish interactions on the competition of resources are poorly investigated. Thus, there is a risk that if fish colonise all created wetlands for biodiversity in a relatively short time, amphibian diversity in this habitat can be reduced due to predation, but also competition and avoidance.

Using the non-invasive technique of environmental DNA (eDNA) metabarcoding as the inventory tool, we surveyed amphibian and fish occurrences in 52 created wetlands in Sweden. Aquatic eDNA is defined as genetic material that has been shed by an organism (extra-organismal DNA) into the surrounding water and can be captured directly from water samples as cellular or subcellular material (Moushomi et al., 2019; Turner et al., 2014; Wilcox et al., 2015). Only a few studies have used eDNA data to test patterns of diversity in wetlands, let alone created ones (see Harper et al., 2020). The advancement of molecular methods makes it possible to identify species in a water column from DNA, enabling a completely new approach for species inventories. Environmental DNA barcoding and metabarcoding have in numerous investigations proven to be successful at detecting cryptic fish species (Hänfling et al., 2016; McElroy et al., 2020; Pochardt et al., 2020; Sigsgaard et al., 2015) and amphibians (Ficetola et al., 2019). By using eDNA, it is also possible to identify those species where morphological identification is hard or impossible (e.g. larvae, Fujii et al., 2019). In studies comparing eDNA sampling and traditional monitoring (gill-net, traps, electrofishing, etc.), the overlap, or repeatability, between taxa detected varies depending on how thoroughly the traditional inventories are performed. However, eDNA analysis is generally comparable to, complementary to or more effective than traditional methods for amphibian and fish detection (Ficetola et al., 2019; Fujii et al., 2019; Hänfling et al., 2016; Lawson Handley et al., 2019; Pont et al., 2019). Therefore, eDNA monitoring alone could be sufficient for evaluating fish and amphibian (Bálint et al., 2018; Harper et al., 2020) communities in created wetlands. Additionally, eDNA metabarcoding as an inventory method is non-invasive and reduces the risk of spreading pathogens, whereas traditional surveys might harm or even kill the target species (Snyder, 2003).

We investigated colonisation patterns and co-occurrences of amphibians and fish in relation to local wetland characteristics, the composition of the surrounding landscape and the species regional pool. For species richness and occurrences of more common species, we predicted: (1) fish to be more likely to occur in wetlands connected with surrounding waterways, while amphibian occurrence would be less dependent on the connectedness of the wetlands (due to their terrestrial dispersal ability); (2) amphibians to be more likely to occur in small wetlands because fish are less likely to occur and prevail in very small wetlands, whereas fish richness should be higher in larger wetlands (area-richness relationship); and (3) amphibians to be less likely to occur in wetlands with a high species richness of fish due to described predatory interactions. To further explore the observed patterns of fish and amphibian occurrence, we also investigated specific pairwise species co-occurrences to better elucidate possible species interactions that might cause amphibian avoidance or exclusion. Last, we compared fish occurrences in created wetlands to pre-existing data on fish occurrences in natural lakes and fish stocking in the same geographical region to better understand which fish species are likely to colonise created wetlands.

2 | METHODS

2.1 | Study sites and environmental data

The sampling of fish and amphibian eDNA took place in June and July of 2018 in 52 created wetlands in the Uppland region (Figure 1), Sweden. These wetlands are generally shallow and were created to promote biodiversity on the whole, but primarily

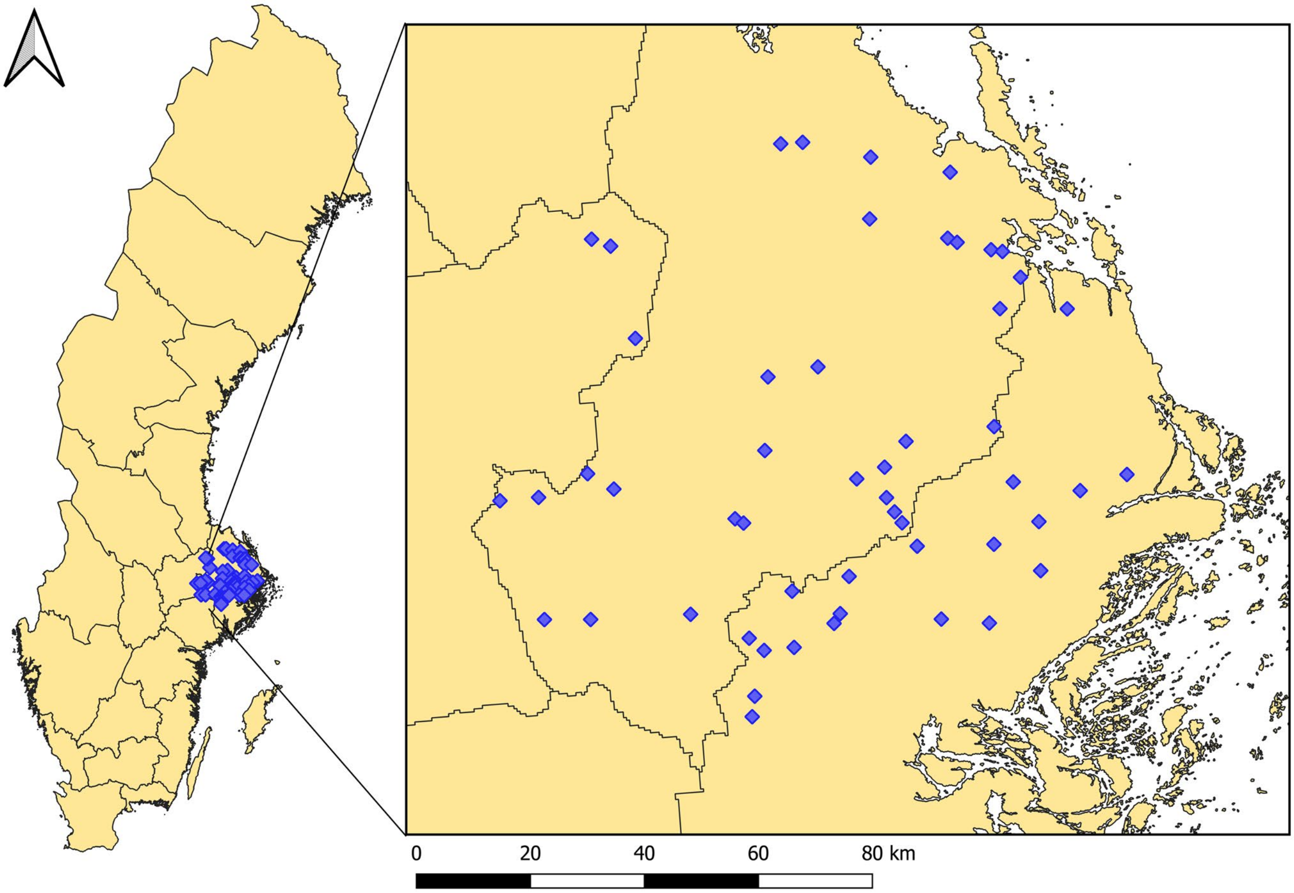


FIGURE 1 Locations of 52 surveyed created wetlands (59°35′3.9″N 16°46′14.3″E; 60°19′37.0″N 18°25′46.4″E; Sweden)

for birds and, to some extent, amphibian diversity rather than fish (Dietrichson, 2017). They were created at sites where no wetland existed at the time of the creation, although some were created at sites where there had historically been a wetland more than 50 years ago. The latter wetlands had been drained, and the land was used for other purposes, usually pastures or arable land. The wetlands in this study were created between 1990 and 2013 (variable 1) and were surrounded by agricultural, forest or urban landscapes (var. 2). Wetland size (var. 3) varied between 0.53 and 20 ha, and wetlands were covered by different percentages of aquatic vegetation (from completely free of to completely covered; var. 4). Many of the wetlands were physically connected (var. 5) via ditches or stream networks to rivers or lakes. The surrounding area around the wetlands is often seasonally flooded, creating temporary pools (var. 6). These selected six environmental variables (local wetland and landscape characteristics) might explain variation in occurrences of fish and amphibians in created wetlands (see Table 1 for details and explanations). All measurements were obtained by digitising hand-drawn maps in ArcGIS software 10.5. Data on the year of wetland creation were obtained by interviewing locals and assessed from aerial photographs repeated since 1990 (Lantmäteriet, 2020). Landscape composition was determined using the Swedish Terrain Map (GSD Geografiska Sverigedata).

Additionally, we extracted data about fish stocking in the Uppland region (Figure 2, Figure S1) based on the permit information given for landowners, which included localities in lakes and rivers, but none of these permits were given for the created wetlands we investigated. Moreover, we obtained data on fish occurrences in 97 natural lakes using fish monitoring surveys (e.g. gill netting) during the last 3 decades, covering the overall study area of created wetlands (see Table S1). Even though the natural systems differ from the created wetlands in size and depth, littoral zone, etc., a comparison between natural and created wetland communities would indicate whether some species might prefer or avoid created wetlands as habitat.

2.2 | Environmental DNA collection and extraction

Prior to the fieldwork, all collection vessels (jars and buckets) were sterilised (using 6%–10% sodium hypochlorite solution) and cleaned. The filtering equipment, including filters and syringes, were ordered in sterile single-use packages. Footwear was cleaned in bleach (10% sodium hypochlorite) before visiting a location, and the collector avoided entering the water. Five litres of water were collected from each wetland from at least ten subsamples, which were spatially and evenly distributed around the pond following Harper et al., (2019). The water collected from the subsamples was mixed in a clean container and double filtered through enclosed double filters made of 5-μm glass fibre and 0.8-μm polyethersulfone membranes (NatureMetrics Ltd) until the water volume reached 3,300 ml or the filters clogged. The median volume of water filtered was 1,500 ml, with water volumes ranging from 210 ml to 3,300 ml (Table S2). Negative field filter controls were taken each sampling day to test for potential field contamination by using bottled water that was filtered on-site and treated like the field samples. All samples were fixated in 96% molecular grade ethanol following Spens et al., (2017) and sent to laboratory

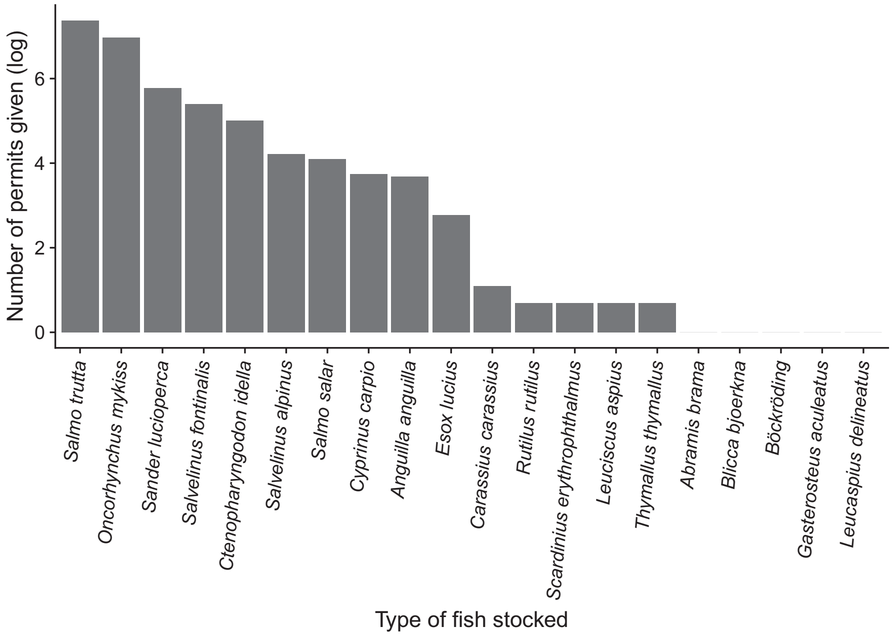
TABLE 1 Environmental variables included in the analysis for fish and amphibian species richness and occurrence

Environmental characteristic	Description (unit)	Explanations	Range (Mean ± *SD*)
Size	The total size of the created wetland water surface (ha)	Larger wetlands may have more species of fish, while amphibians will be more likely to occur in smaller wetlands	0.53–19.98, (4.57 ± 3.99)
Water vegetation	Cover of wetland area by emergent water vegetation (e.g. *Typha*, *Phragmites*, *Iris*) and floating water vegetation (e.g. *Nymphaea*, *Lemnoideae*, algae; %)	Habitat and possible refuges for amphibians, structural complexity, reflects water productivity, general depth of a wetland	0–98.2, (50.1 ± 30.4)
Connectivity	Whether the wetland has ditches/streams that connect it to other water bodies (except for dams which are assumed to be isolated in terms of natural fish colonisation probability)	Connectivity makes wetlands colonisable by fish	28 connected, 24 isolated
Flooded area[a]	The proportion of area around the wetland shore that is flooded (50 meters around wetland shore) (%)	Protection from predators and more suitable habitat for amphibian eggs and larvae	0–55.6, (12 ± 12)
Year of creation[b]	The year when the wetland was created. When this information was not available, the age was estimated using aerial photographs.	Time allows more species to colonise and establish	1990–2013, (2001 ± 5.6)
Landscape forest	Coverage of forest within 1 km buffer starting from the wetland shore (%)	May affect wetland acidity and productivity	0.5–100, (66 ± 24.6)

[a] Not applied for fish.

[b] not applied for amphibians as they are able to colonise wetlands during the first years of creation, and all wetlands in this study were at least 5 years old at the time of the survey (Lesbarrères et al., 2010; Petranka et al., 2003).

FIGURE 2 The frequency of stocking permits given for each species in the Uppland region (see Figure S1). In Sweden, the stocking permit is required just for connected wetlands, but none of our inventoried connected wetlands had received such permits



(MoRe Research AB), designated for eDNA purposes only, for extraction following a modified protocol for enclosed filters in Spens et al., (2017). The modification included pooling the lysate after the overnight lysis of the filter capsule DNA and ethanol pellet DNA into one sample in order to gain a higher DNA yield. The extracted DNA samples were sent to a commercial laboratory, NatureMetrics Ltd, for downstream analytical applications, including polymerase chain reaction (PCR), high-throughput sequencing, and bioinformatics (see Appendix S1 for more details). We used MiFish 12S primers (Miya et al., 2015, 2020) and additionally adjusted MiFish primers to match amphibians on the 12S region (for details, see Appendix S1.1). For each step in the pipeline ranging from field collections to PCR, controls were introduced and were treated like the original samples. The control samples used were as follows: negative filter controls in the field, negative extraction controls (one for every 20 samples), negative PCR controls and positive PCR controls (mock community of tropical fishes). All the controls were amplified and sequenced. A detailed description of the 173 negative and 12 positive controls is given in Appendix S1.1.

2.3 | Statistical analyses

We used generalised linear models to examine the variation in fish and amphibian species richness (Poisson distribution), and additionally, variation in occurrence (binomial error distribution) for some of the more common fish (e.g. species occurring in >10 sites) and all amphibian species at our study sites, using five out of total six environmental variables relevant for either fish or amphibians (Table 1). A species was assumed to occur at a site when we detected eDNA sequences from it and was considered absent if eDNA of that species was not detected (the minimum number of reads per species was 55 for fish and 33 for amphibians). In the models analysing amphibian species richness, we additionally added fish species richness as an explanatory variable.

We used the *co-occur* package (Griffith et al., 2016) to infer associations between fish and amphibian species based on presence–absence data. The co-occur package investigates observed co-occurrences in relation to a null hypothesis of random species distributions without accounting for environmental data. We excluded those species that occurred in three or fewer sites (nine fish species excluded, analysed 14 remaining species, including all amphibians) for these analyses. Additionally, we performed non-metric multidimensional scaling (NMDS) for analyses of community structure following environmental gradients using two dimensions, which can facilitate the interpretation of species distributions. The presence/absence species data were analysed using the Bray–Curtis distance measure and the metaMDS function in the *vegan* package (Oksanen et al., 2019). For NMDS only, we excluded the occurrence of rainbow trout *Oncorhynchus mykiss* as it is non-native and appeared singularly in one wetland, thus acting as rare species in the ordination analyses and appearing outside the species ordination cloud. All analyses were done in R software version 3.6.0 (R Core Team, 2019).

3 | RESULTS

The in-silico testing of the MiFish fish 12S primers could immediately distinguish 17 of the 18 fish species included in the analyses in this study. The MiFish primers adapted to amphibians detected five unambiguous amphibian species (see Appendix S2 for more details and Table S3 for the operational taxonomic unit sequences). The eDNA metabarcoding results showed that none of the negative control samples contained any fish or amphibian DNA that were the target species for the metabarcoding pipeline. The DNA was expectedly very inhibited and purified to remove PCR inhibitors using a commercial purification kit. The DNA concentrations were measured after cleaning and sufficient for analyses. The results from field and laboratory quality controls, amount of water collected per sample and detailed sequencing results are outlined in Supplementary information, Appendix S2.

In total, we detected 18 fish species in the 52 investigated wetlands (Figure 3, Figure S2, Table S4). The most common fish species was nine-spined stickleback *Pungitius pungitius* (found in 20 wetlands), followed by Eurasian perch *Perca fluviatilis*, northern pike *Esox lucius* (each at 19 wetlands), Eurasian roach *Rutilus rutilus* (18), Crucian carp *Carassius carassius* (14), and three-spined stickleback *Gasterosteus aculeatus* (13). Three species were detected only once. Out of 32 fish species in the region, 15 were not detected in the created wetlands (Table S5).

We detected no fish species at three of the wetlands. At the other 49 wetlands (Figure S2), we found that the number of fish species ranged from one (18 wetlands; commonly *P. pungitus*) to 10 (one wetland), with a median of two. The frequency distribution of fish species richness was therefore skewed towards most wetlands having few species. The occurrence of some fish species in created wetlands reflected the occurrences of fish species at the regional level as judged from the long-term data from fish surveys in natural lakes (Figure 4, Table S1). However, many species of fish occurred infrequently in both created and natural wetlands, while others showed a mismatch between the frequency of occurrences between created and natural systems. Even though species such as *R. rutilus* and *P. fluviatilis* were common in both inventories, species such as common bream *Abramis brama* or ruffe *Gymnocephalus cernua* that are frequent in natural systems were rare in the created wetlands, while species such as *P. pungitius* and *G. aculeatus* were commonly found in created but not in natural wetlands.

We detected five amphibian species; the most frequently found was the common toad *Bufo bufo* (34 wetlands, Figure 3, Figure S2), followed by the smooth newt *Lissotriton vulgaris* (31) and great crested newt *Triturus cristatus* (16), while moor frog *Rana arvalis* (11) and common frog *Rana temporaria* (10) were least common.

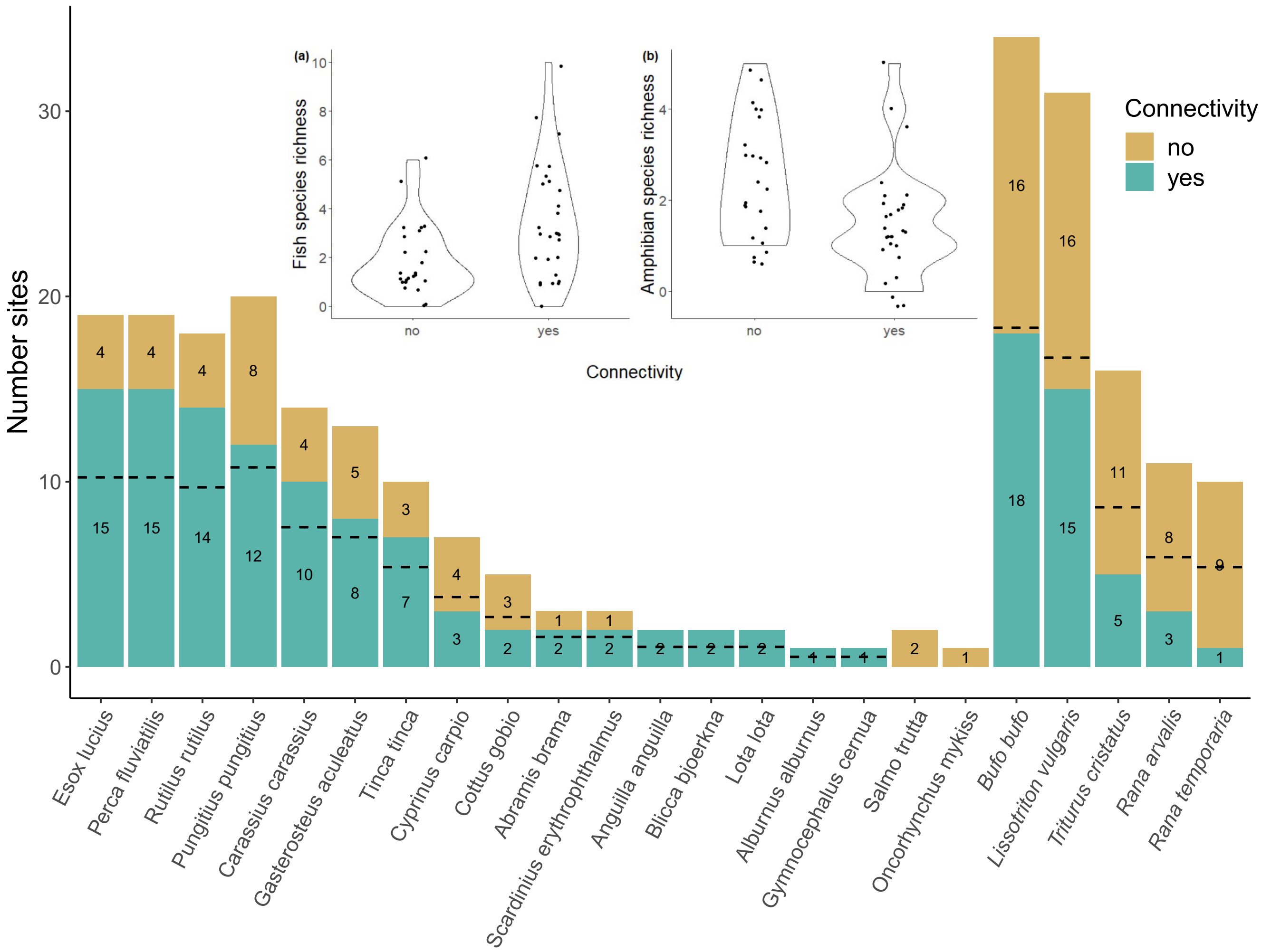


FIGURE 3 Fish and amphibian species occurrences in connected (turquoise) and isolated (dark yellow) wetlands. The black dashed lines indicate the number of wetlands a species would occur in connected wetlands if the occurrence had been random. The violin plots in the top illustrate (a) fish species richness and (b) amphibian species richness in isolated and connected wetlands. Of the 52 wetlands, 28 were connected and 24 isolated

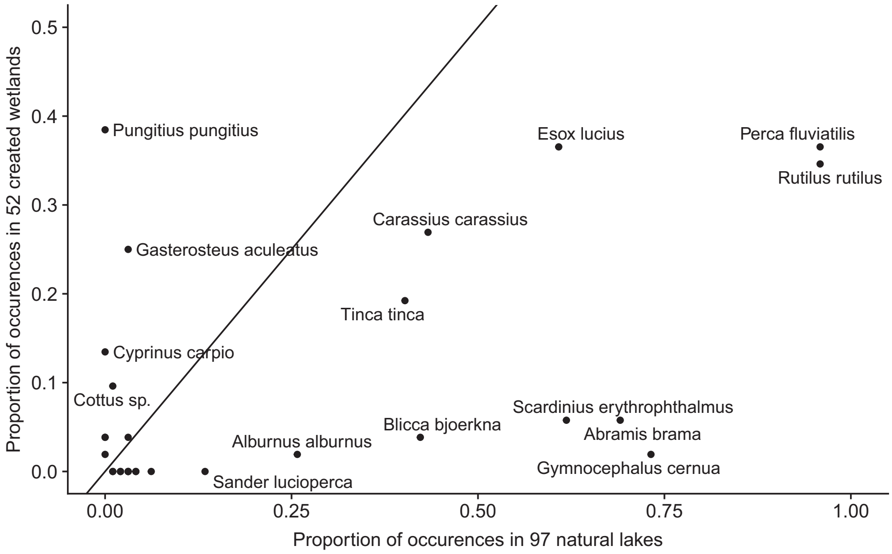


FIGURE 4 The comparison of species occurrence frequencies between the 52 created wetlands using eDNA data from the year 2018 (this study) and 97 natural lakes, surveyed by gill mesh nets within the Uppland region. Black line represents identity line (i.e. 1:1). Species occurring in low frequencies (<4 sites) are not labelled but include *Abramis ballerus*, *Anguilla anguilla*, *Aspius aspius*, *Cobitis taenia*, *Coregonus albula*, *Coregonus lavaretus*, *Cyrpinidae* sp. (only for 2 natural lakes), *Leuciscus idus*, *Leuciscus leuciscus*, *Lota lota*, *Oncorhynchus mykiss*, *Osmerus eperlanus*, *Salmo trutta*, and *Squalius cephalus*

TABLE 2 Model estimates for each included environmental variable in relation to fish and amphibian species richness [95% confidence interval]

	Fish	Amphibians	Amphibians
Wetland size^{a}	−0.01 [−0.19, 0.17]	−0.00 [−0.21, 0.20]	−0.00 [−0.20, 0.20]
Water vegetation	0.11 [−0.07, 0.29]	0.19 [−0.00, 0.39]	0.21* [0.01, 0.40]
Flooded area		0.04 [−0.16, 0.25]	0.03 [−0.18, 0.24]
Connectivity	0.67*** [0.30, 1.04]	−0.54** [−0.94, −0.13]	−0.47* [−0.92, −0.02]
Year of creation	0.02 [−0.16, 0.20]		
Landscape forest	−0.19* [−0.34, −0.04]	0.10 [−0.12, 0.32]	0.08 [−0.14, 0.31]
Fish richness			−0.09 [−0.33, 0.16]
AIC	207.83	172.71	174.21
N	52	52	52
Pseudo r^2	0.36	0.20	0.21

All variables were mean centred and scaled.

Abbreviation: AIC, Akaike information criterion

^{a}Log-transformed.

$^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

The only species occurring in the region that was not found in our eDNA samples is pool frog *Pelophylax lessonae*, which only breeds at the north-eastern coastal part where we did not sample (Figure 1). The frequency distribution of amphibian species richness was also skewed; most commonly, wetlands were inhabited by just one species (18 wetlands), but three wetlands had all five species (Figure S2). Five wetlands were amphibian-free.

3.1 | Fish occurrence patterns

Fish species richness in created wetlands was related to wetland connectivity and the proportion of forest within one kilometre. On average, fish species richness was predicted to be twice as high (confidence interval [CI] = [1.4; 2.8]) in connected (predicted number of species [CI] = 3.43 [2.73; 4.13], when keeping other variables in their means) as compared to isolated wetlands (1.76 [1.19; 2.33], Table 2, Figure 3a). Fish species richness was 53.7% [32.9; 88.5] lower in forest-dominated landscapes (90% forest cover, Table 2, Figure S3d) than in unforested ones (10% forest cover).

Similarly to the results for fish species richness, when investigating fish species individually, most species tended to occur more frequently in connected wetlands (e.g. *E. lucius*, *P. fluviatilis*, *R. rutilus*, *C. carassius*; Figures 3 and 5), and the occurrence of the most common species *P. fluviatilis* and *C. carassius* was related to landscape type with these species occurring less frequently in more forested wetland locations (Figure 5, Figure S4h,t). Furthermore, the occurrence of two species was related to wetland size; *P. pungitius* occurred more frequently in large wetlands (Figure 5, Figure S4a), while *C. carassius* only occurred in small ones (Figure 5, Figure S4q). *Carassius carassius* occurred more often in less vegetated wetlands (Figure 5, Figure S4r) and more often in older wetlands (Figure 5, Figure S4s), alhough the estimates for this species are very uncertain (large CI) and thus have to be viewed with caution.

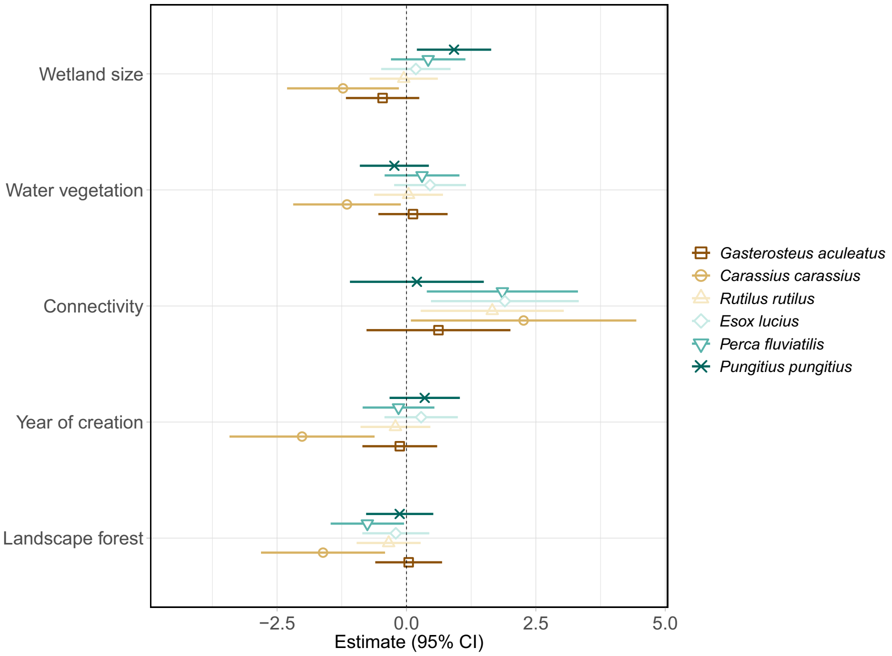


FIGURE 5 Model estimates for each environmental variable (centred and scaled) included in relation to the occurrence of the six most common fish species. Error bars represent 95% confidence intervals (CI). Wetland size was log-transformed

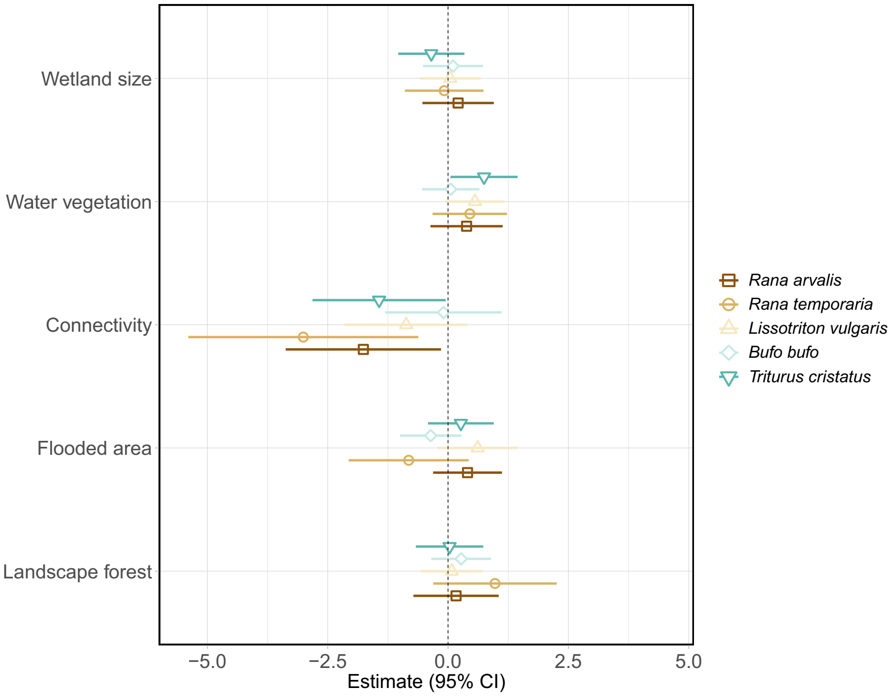


FIGURE 6 Model estimates for each considered environmental variable (centred and scaled) in relation to the occurrence of each amphibian species. Error bars represent 95% confidence intervals (CI). Wetland size was log-transformed

For effect plots of all species and environmental variables, see Figures S3-S4.

3.2 | Amphibian occurrence patterns

Contrary to the pattern found in fish, model estimates indicated amphibian species richness was 41.5% lower (effect size 0.6 [0.39; 0.88] CI) in connected wetlands (predicted number of species [CI] = 1.45 [1; 1.90], when keeping the other variables at their means) than in isolated ones (2.47 [1.77; 3.18], Figure 3b, Table 2). Amphibian species richness was positively associated with the proportion of water vegetation (Table 2, Figure S3f), where species richness was 59.9% [35.3; 100.2] higher in wetlands with high cover of water vegetation (90% cover of the wetland) than in those with low water vegetation (10% cover). When looking at species individually, the negative relationship to wetland connectivity (less frequent in connected wetlands) was evident for occurrences of *T. cristatus*, *R. arvalis*, and *R. temporaria*, but not for *B. bufo* and *L. vulgaris* (Figures 3 and 6). The positive relationship to the proportion of water vegetation was especially clear for the occurrence of *T. cristatus* (Figure 6, Figure S5b). Other environmental variables did not show clear relationships with amphibian occurrence (Figure 6, Figures S3 and S5).

Additionally, observed fish species richness did not clearly explain variation in amphibian species richness when added to the full model, i.e. model Akaike information criterion value increased when fish richness was included (Table 2, Figure S6). As toads are poisonous and might not be preyed upon by fish, we also analysed amphibian richness omitting *B. bufo*; however, such analyses did not change our conclusions concerning the lack of fish–amphibian association (fish richness estimate −0.1 [−0.4, 0.21]).

3.3 | Fish and amphibian co-occurrence

According to the probabilistic species co-occurrence analyses (Figure 7), which identified 91 species pairs, 14 (15.4%) co-occurrences were significantly positive, five (5.5%) significantly negative, and 72 were not statistically clear (79.1%). All negative co-occurrences were between fish and amphibians, while positive pairwise occurrences were within the fish community (7), within the amphibian community (4), or between amphibians and fish (3). *Triturus cristatus* occurred more often with European bullhead *Cottus gobio* (co-occurred 4 times, expected to co-occur 1.5 times under the null hypothesis of random associations), common carp *Cyprinus carpio* (co-occurred 5, expected 2.2), and *G. aculeatus* (co-occurred 7, expected 4). By contrast, *T. cristatus* occurred less frequently with *E. lucius* (co-occurred 2, expected 5.8), tench *Tinca tinca* (co-occurred 0, expected 3.1) and *P. pungitius* (co-occurred 3, expected 6.2). *L. vulgaris* presence was less likely in the presence of *T. tinca* (co-occurred 3, expected 6). *R. temporaria* presence was also less likely in the presence of *C. carassius* (co-occurred 0, expected 2.7). *R. arvalis* and *B. bufo* did not show higher than expected co-occurrence pattern with fish (see also Figure S7). When it came to within taxa co-occurrences, i.e. either between fish species or between amphibian species, none of the co-occurrences were significantly negative.

NMDS analyses showed a significant distinction between community composition in connected and isolated wetlands (Figure 8, Figure S8, $r^2 = 0.09$, $p = 0.006$, centroid for isolated: −0.0218 [NMDS1], −0.2286 [NMDS2], connected 0.0187 [NMDS1], 0.1959 [NMDS2]), although it was a weak predictor (stress = 0.2). Other environmental variables did not show a correlation with the community assemblage gradient. Amphibians were concentrated in the central bottom part of the diagram (except for *B. bufo*), while species in the fish community were scattered around in the ordination space with more concentration to the top part of the diagram. Thus, amphibians showed a higher degree of niche similarity as compared to fish.

4 | DISCUSSION

We found fish species richness to be higher in connected wetlands, while the opposite was true for amphibian species richness. Additionally, amphibian occurrences showed a more aggregated pattern in the ordination analyses compared to the scattered pattern of fish occurrences. These different patterns in environmental space use might indicate negative associations between fish and amphibians, as we also observed some negative pairwise fish–amphibian co-occurrences. Still, out of the 52 surveyed wetlands, fish and amphibians did co-occur at 44 sites. However,

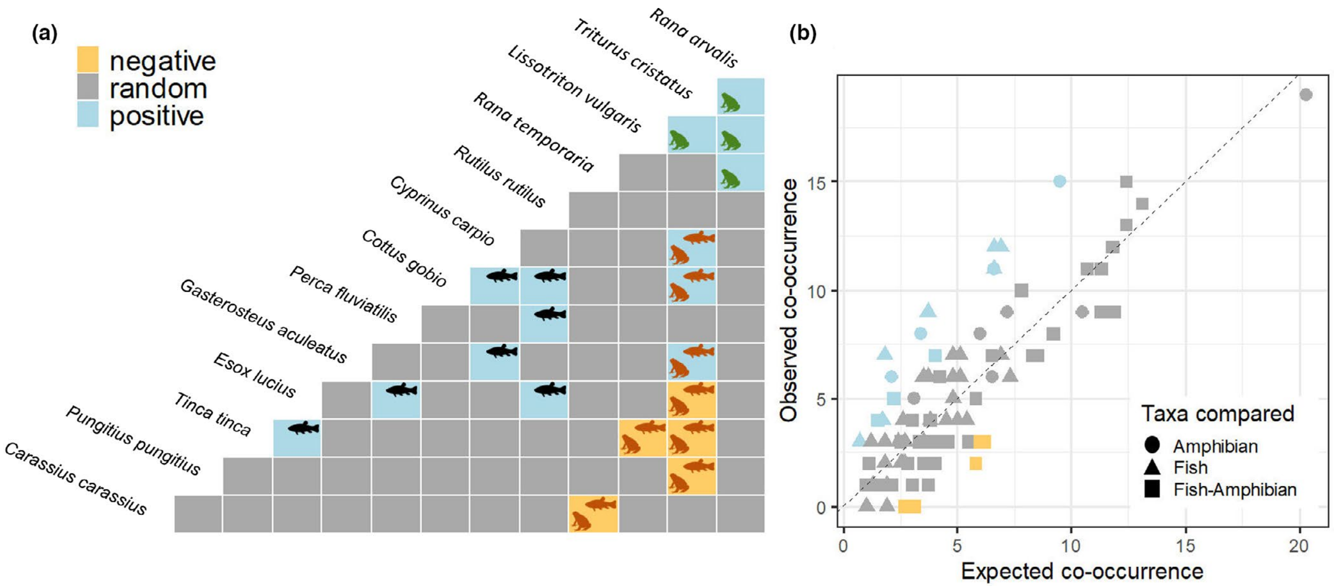


FIGURE 7 (a) Probabilistic species co-occurrence matrix and (b) observed-expected plot. Colours represent negative (yellow), positive (blue), and random (grey) species associations. Yellow and light blue colours indicate significant, above 0.95, probabilities. For illustration purposes, associations within amphibians (green, circle) and fish (black, triangle), and between amphibians and fish (brown, square) are marked with appropriate colours and shapes. We excluded species occurring in three or fewer wetlands (*Alburnus alburnus*, *Abramis brama*, *Anguilla anguilla*, *Blicca bjoerkna*, *Gymnocephalus cernua*, *Lota lota*, *Oncorhynchus mykiss*, *Salmo trutta*, *Scardinius erythrophthalmus*), while species with only non-significant associations are not illustrated (*Bufo bufo*, *panel a*)

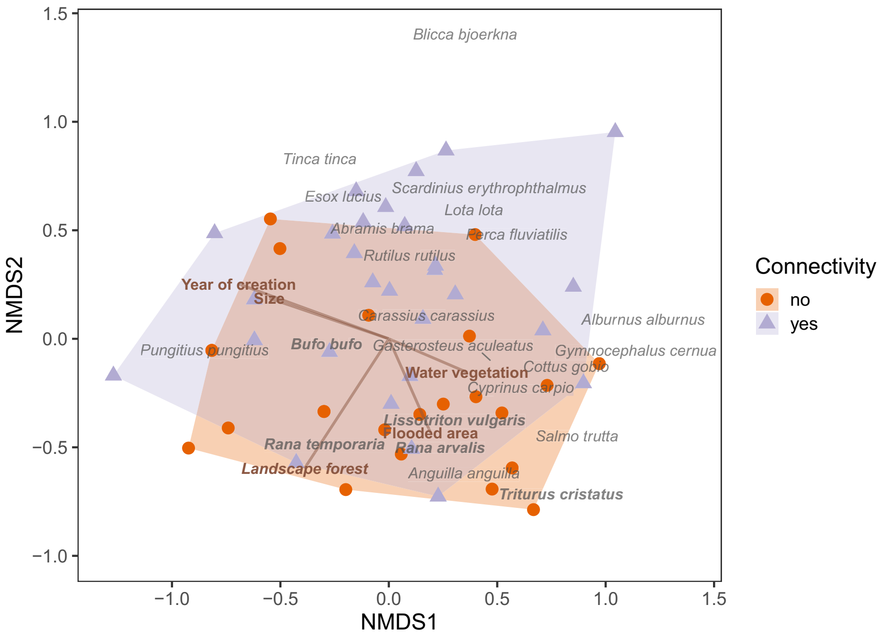


FIGURE 8 The non-metric multidimensional scaling (NMDS) plot of all wetlands (stress 0.2) shows the clustering of communities within connected and isolated wetlands. The arrows show the five fitted environmental gradients; however, none of them were significant. Triangles and circles represent connected and isolated wetlands; shaded areas are the convex hulls of the triangles and points, respectively. Rainbow trout (*Oncorhynchus mykiss*) was excluded because it is non-native and occurred in one wetland only

fish–amphibian co-occurrence when *B. bufo* is excluded, because it is poisonous, dropped to 31 sites (see below). Therefore, we cannot rule out that fish–amphibian interactions may be of importance when amphibians colonise wetlands created for biodiversity. However, the high frequency of fish–amphibian co-occurrences suggests that any pattern of amphibian avoidance or exclusion by fish might be counterbalanced by other characteristics of the wetland, enabling the co-occurrence of these two species groups.

Although we found all amphibian species expected to be in the surveyed created wetlands, we found 17 (out of which two are non-native) fish species expected to also occur in the region, which is 53% of the total species pool. Of these fish species, some were more common while others rarer in created compared to natural wetlands. Such differences between fish species communities in created and natural wetlands may come from specific species adaptations and niche requirements but also from the different inventory methods used. As eDNA metabarcoding may detect species that would be missed by conventional methods to survey fish, our results contribute to the general knowledge of amphibian–fish species co-occurrence patterns, especially so for the associations with small-bodied fish as these may go undetected when using conventional survey methods (see below).

4.1 | Fish occurrence patterns

Connectivity, that is, the physical connection to other waters, was an important predictor associated with fish species richness and occurrence, as more species were found in connected compared to isolated wetlands. This does not come as a surprise, as physical connectivity makes colonisation easier for fish (Hammer, 1992; Streever & Crisman, 1993). Additionally, methane (indicating anoxia) is significantly correlated with variation in fish community composition in isolated Swedish wetlands (Öhman et al., 2006) as it reduces long-term fish survival. Still, isolated wetlands were able to support up to six fish species with 1.8 species on average. One of the most obvious explanations for the occurrences of some fish species in created wetlands is stocking (cf. Søndergaard et al., 2018), and in Sweden, fish stocking permits are not required for isolated water bodies (SFS, 2020). Therefore, it is likely that some of these occurrences were due to stocking, especially when it comes to non-native species and in isolated wetlands. However, fish occurrence in isolated wetlands could also be related to the creation process, when fish are trapped at the initial filling of a wetland (cf. Snodgrass et al., 1996) or through irrigation (Langston & Kent, 1997) or natural causes, such as terrestrial dispersal (European eel *Anguilla anguilla*, Bergmann, 1978) or flooding events (e.g. *A. brama*, Grift et al., 2001).

When considering the fish species pool in natural lakes of this region, many species were rare in both created and natural wetlands. A few species—*P. fluviatilis*, *E. lucius*, *R. rutilus*, and *C. carassius*—were relatively common in natural lakes and created wetlands. Yet other species common in natural lakes were almost absent in created wetlands. Created wetlands usually are shallow and lack a large pelagic zone, and, therefore, some fish species adapted to large, open or deep waters will not thrive in the created wetlands (e.g. bleak *Alburnus alburnus*). By contrast, few fish species occurred more often in created than in natural wetlands, such as *P. pungitius*, *G. aculeatus*, *C. carpio*, and *C. gobio*. *P. pungitius* and *G. aculeatus* are among the smallest fish species in this region and thus are often missed in the surveys using multi-mesh gill-nets (also used for the natural lake surveys). The catchability of different fish species differs; however, eDNA from these small species was obviously detected in the created wetlands. Additionally, the conditions in created wetlands might be beneficial for species that have a high tolerance to hypoxic conditions (such as

C. carassius and *C. carpio*, e.g. Nilsson & Renshaw, 2004; VanRaaij et al., 1996).

Regardless of the source for fish colonisation, some species will initially flourish but might disappear after some time (cf. Degani et al., 1998); therefore, other habitat characteristics not related to colonisation will partly determine whether fish will establish and thus be possible to detect. However, wetland size was not distinctly related to species richness in contrast to what we expected (i.e. due to species–area relationship). This suggests that size does not limit the fish species community or that created wetlands are too small for seeing the species–area relationship, as created wetlands had half of the regional species pool. We also did not find support for our expectation of older wetlands to have more species. This could be because the youngest wetland in our study was at least 5 years old, where most of the species may already have colonised the created wetlands at the time of our surveys (cf. fast colonisers of created wetlands, Kristensen et al., 2020). Additionally, confidence intervals are wide and cover a range of non-trivial effect sizes, and we cannot exclude the possibility that we simply were not able to detect the effect.

The fish community was associated with the landscape context as wetlands with a high proportion of forest in the surroundings tended to have fewer species and occurrences of two species (*C. carassius* and *P. fluviatilis*). During spring, organic acids are usually washed out into the wetlands (minimum pH; cf. Laudon et al., 2000); therefore, wetlands in the forested landscape may be rather acidic compared to those located in agricultural land, as the latter land-use increases soil pH and thus surrounding water bodies (Renberg et al., 1993). Some fish tolerate acidity, but even acid-tolerant *P. fluviatilis* and *C. carassius* occurred less often in wetlands located in a forested landscape. Alternatively, wetlands in open areas (e.g. non-forested) in the flat Uppland region may be more prone to flooding than those in forested areas, thus wetlands in non-forested landscapes may be more easily colonised by fish.

4.2 | Amphibian occurrence patterns

Avoidance of, or exclusion by, fish is one explanation to why species richness and occurrence of *T. cristatus*, *R. temporaria*, and *R. arvalis*, were higher in isolated wetlands compared to fish-rich connected ones. As illustrated by the NMDS analysis, amphibian species, except *B. bufo*, display a narrower environmental niche space than the fish community. Predatory fish can completely deplete the amphibian larvae from the wetland (Heyer et al., 1975). Therefore, predatory fish are usually negatively related to the amphibian presence (Porej & Hetherington, 2005), but this is not always the case, especially when the fish present are native (Pearl et al., 2005). *Bufo bufo* is an exception from this pattern as this species is toxic and is not usually preyed upon by fish (Manteifel & Reshetnikov, 2002) and can even prefer ponds with fish (Beebee, 1979). Although unlikely, we cannot rule out alternative explanations for the amphibian preference of isolated wetlands, for instance, inflow could contribute to the influx of pollutants from agricultural fields (Harper et al., 2020), for which amphibians would be sensitive.

In general, out of the nine fish species analysed, only four species displayed a clear negative association with amphibians, of which *E. lucius* could be directly linked to predation, while the other three fish species are probably linked to the competition for food (cf. Reshetnikov, 2003). Similarly to other research (Harper et al., 2020; Magnus & Rannap, 2019), *T. cristatus* was most sensitive to the presence of fish (i.e. three negative associations with fish). However, amphibians often co-occurred with fish, and there were also several positive associations between amphibians and fish, although only with *T. cristatus* (three positive associations). This latter result contrasts the claims that *T. cristatus* altogether avoid fish (Magnus & Rannap, 2019; Skei et al., 2006). Some of the fish species positively co-occurring with amphibians could reduce amphibian larva predation by consuming their predators, including predatory insects (Brown et al., 2012), such as *Aeshna* dragonfly larva (Laurila et al., 2008) or other Odonata species (Johansson & Brodin, 2003). The general amphibian co-occurrence with fish could also reflect variation in habitat quality and productivity. For example, a higher cover of water vegetation is generally important for amphibians as it provides breeding habitat and protection from predators (Shulse et al., 2012). Water vegetation cover was positively related to amphibian species richness and at least to the occurrence of *T. cristatus*, which is in line with previous studies (Brown et al., 2012; Hecnar & M'Closkey, 1997; Shulse et al., 2012). However, some species' relatively low occurrence frequencies reduce the power to detect interspecific associations, which is why an absence of a clear co-occurrence pattern within and between fish and amphibians investigated should be taken with quite some care.

Several studies suggest that many amphibian species prefer small wetlands because fish are more likely to be absent because of unfavourable conditions for fish survival (Harper et al., 2020; Semlitsch et al., 2015). However, we did not find any clear relationship between wetland size and richness or occurrence of amphibians. All our sampled wetlands, however, were larger than 0.5 ha, while the suggested optimal size for many amphibian species may be as small as 0.1 ha (Semlitsch et al., 2015; but see Bancila et al., 2017). Therefore, similarly to studies involving larger ponds (Landi et al., 2014; Porej & Hetherington, 2005), we may have failed to detect such a preference for the smallest wetlands as these were not available in our study area. Furthermore, as most wetlands had fish, probably because they were large enough not to dry out entirely or freeze, we may lack relevant variation in wetland size to detect the amphibian preference for smaller, fish-free wetlands. We also predicted flooded areas creating temporary pools to positively relate to amphibian species as it could provide shelter from predators (Porej & Hetherington, 2005; Tramer, 1977). We found no such clear relationship, probably due to increased connectivity for small-bodied fish (Lyon et al., 2010).

Finally, in contrast to fish, amphibians displayed no clear relationship to the landscape setting of created wetlands, despite the suggestion that forest cover is a positive predictor for amphibian occurrence (Pearl et al., 2005), either due to dispersal facilitation (Brown et al., 2012) or improved water quality (Simon et al., 2009). The lack of correlation here could be because the Uppland region is rather forested and does not lack moist areas for dispersal and all five species detected in the created wetlands were widespread in this region (Swedish Species Information Centre, SLU, 2020).

4.3 | Study limitations when using eDNA metabarcoding

As with any other field survey methods, despite numerous investigations demonstrating that eDNA metabarcoding as a tool to detect amphibian and fish species is an efficient and precise survey method (Lopes et al., 2021, Miya et al., 2020), the use of eDNA analyses has its limitations. First, wetlands are usually rich in humic acids, which easily interfere with molecular analyses (Matheson et al., 2010). The samples in this survey were inhibited, and the inhibition removal process may have reduced the available DNA for sequencing, thus reducing overall detection probability (but see Appendix S2 for comparison with other studies). Second, in this survey we used Miya et al., (2015) MiFish primers for fish and adapted them towards amphibians' 12S region on the reverse primer to avoid amphibian presence being masked by fish. Even though this reduces the risk, there is still a possibility that amphibian species with low eDNA abundance in these ponds may be underrepresented, and other mitochondrial DNA regions might be more suitable (e.g. 16S region). The common and widespread species *R. arvalis* and *R. temporaria* occurred perhaps less frequently than expected, while *T. cristatus* was more frequent in our study sites. Thirdly, falsely detected occurrences (e.g. *Clupea harengus* and *Gadus morhua*) are usually a consequence of contamination from sewage, recreation, excrements from fish-eating birds (Guilfoyle & Schultz, 2017) and by water inflow from adjacent wetlands harbouring fish (Hänfling et al., 2016; Harper et al., 2020), which could have influenced our interpretation of fish presences in connected wetlands or wetlands close to recreational places, although fast degradation of eDNA reduces such risk. Last, we do not have data on fish age that in turn would inform us about fish cohort structure, which could affect predation risk patterns (Kloskowski, 2009).

Nevertheless, eDNA metabarcoding is a powerful tool to detect common species, and, particularly efficient in detecting species that are elusive, static, or rare (Bálint et al., 2018; Hänfling et al., 2016), hard to detect or identify (e.g. early developmental stages, Fujii et al., 2019; Lopes et al., 2017), or, in general, species with low catchability with standard methods, such as multi-mesh gill-nets (Sutela et al., 2008).

5 | CONCLUSIONS

When creating wetlands to facilitate biodiversity, fish is not usually a target taxon. Still, fish come almost always with the water, either by natural colonisation through watercourses (i.e. connectivity) or by stocking. As partly suggested by our study, fish presence may impact the wetland use by communities of other wetland taxa, such as amphibians, based on the observed opposing preferences of connected and isolated wetlands. However, our study also suggests that fish and amphibians can co-exist. The creation of larger wetlands and increased habitat heterogeneity in terms of water vegetation, and shape and structure of the wetland could be possible factors enabling the co-existence of these two taxa, but this requires further studies.

Environmental DNA metabarcoding is a relatively cheap and time-efficient method to conduct surveys of fish and amphibian species occurrences in wetlands. Furthermore, the non-invasive eDNA surveys would also include small-bodied fish that otherwise might be missed by conventional fish surveys using multi-mesh gill-nets. The knowledge about fish community assemblages in created biodiversity wetlands using eDNA metabarcoding, thus provides new and detailed insight into fish occurrence patterns and possible associations with amphibians and other taxa to improve the future creation of wetlands for biodiversity.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from Swedish National Data Service: https://doi.org/10.5878/gzq7-8q71

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SUPPORTING INFORMATION

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To mitigate wetland biodiversity declines caused by wetland destruction and degradation, wetlands have been created and restored worldwide. As we lack large-scale evaluations, this thesis explores local and landscape effects to infer community responses to wetland creation and restoration. Created wetlands attracted most species of the regional freshwater bird, amphibian and fish community. Wetland restorations increased half of the local bird populations. This thesis informs how wetland creation and restoration can be improved to achieve cost-effective conservation actions.

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