



# Community associations of birds with amphibians and fish in wetlands created for biodiversity

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## ABSTRACT

Conservation initiatives to support declining water-related biodiversity through wetland creation have increased during the last decades. Multiple studies have evaluated the suitability of created wetlands for birds and amphibians, but only a few have considered the species associations that might also affect the outcome. Using joint species distribution models, we explored species associations of birds, amphibians and fish in 52 created biodiversity wetlands in Sweden. As most of these wetlands were primarily created for increasing bird diversity, we asked whether the occurrence of fish and amphibians relates to bird species richness, pair abundance and chick abundance (as a measure of reproductive success) and whether conservation conflicts or synergies between birds, amphibians and fish can be observed. In general, we found positive bird-amphibian association patterns and negative bird-fish association patterns, although the uncertainties were high for these estimates. In line with previous research, the generally negative bird-fish co-variance indicates potential conservation conflicts between wetland creation for birds and fish, where fish might be introduced for recreational fishing or other ecosystem services. Therefore, our results suggest that it can be hard to benefit bird and fish communities with the same wetland, and separate wetland creation with different goals may be needed. The generally positive bird-amphibian species-species associations and the lack of previous studies revealing conflicts indicate synergies between wetland creation for birds and amphibians. However, research needs to further consolidate such synergies, including amphibian reproductive output from bird-rich wetlands.

## 1. Introduction

Humans have destroyed around two-thirds of natural wetlands (Davidson, 2014), and many of the remaining ones are deteriorating (Zedler and Kercher, 2005). To reverse this loss, wetland creation is accelerating (e.g. Niu et al., 2012), and today created wetlands can comprise a large part of total wetland areas (e.g. 20 % of wetlands in the USA are created, Smith et al., 2002). The reasons for creating wetlands can be diverse, e.g. creating water reservoirs for agricultural irrigation, nutrient retention from agricultural runoff, reclamation of quarry sites (McKinstry and Anderson, 2002; Sánchez-Zapata et al., 2005; Strand and Weisner, 2013; Tourenq et al., 2001), and often for the benefit of wetland-related biodiversity (Magnus and Rannap, 2019). Birds and amphibians are a common target when creating biodiversity wetlands (Sebastián-González and Green, 2016; Magnus and Rannap, 2019). The focus on improvement for these two taxa is usually motivated by the fact

that 55 % of wetland bird and 43 % of amphibian species are in decline worldwide (BirdLife International, 2017; Stuart et al., 2004). On the other hand, fish are rarely the primary focus of wetland creation to promote biodiversity, but fish could have a negative impact on bird and amphibian conservation (see also below; Brown et al., 2012; Dessborn et al., 2011; Elmberg et al., 2010; Magnus and Rannap, 2019; Ortuabay et al., 2006). Thus, wetland creation promoting one group of species may come at the cost of negative effects on other species groups. In a more optimistic scenario, however, biodiversity management of one group of species might benefit other groups of species (Maskell et al., 2013). Therefore, conservation synergies and conflicts must be identified to avoid counter-productive wetland creation and increase the wetland creation benefits if synergies are observed.

The colonisation of new wetlands by a particular species or taxon may depend not only on the habitat characteristics but also on other species and taxa present due to species interactions such as predation

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and competition. Bird, amphibian and fish species are likely to interact with each other, which in turn could affect their habitat use and co-occurrence patterns, thus potentially affecting the success when creating wetlands for biodiversity. For example, piscivorous birds should benefit from the presence of fish (usually smaller fish; Lammens, 1999; Ortubay et al., 2006; Kloskowski, 2012; van Eerden et al., 1993), but other parts of the wetland bird community could be negatively associated with fish due to competition for similar food sources (Eriksson, 1979; Kloskowski and Trembacowski, 2015; Kloskowski, 2012) or predation of mainly chicks of smaller species (e.g. Northern pike *Esox Lucius*, Dessborn et al., 2011; Elmberg et al., 2010; Paasivaara and Pöysä, 2008). Broad bird-amphibian associations are likely to be mainly weak, although birds foraging on adult amphibians might lead to more frequent co-occurrences (Toledo et al., 2007) that may not lead to local amphibian extinction and with no evidence for strong competition. On the other hand, amphibians are often reported to be negatively associated with fish due to more frequent predation (Hartel et al., 2007; Heyer et al., 1975). Also, at least within the bird community, positive species associations may occur due to heterospecific attraction leading to multi-species aggregations (Šálek et al., 2022; Sebastián-González et al., 2010), such as in herons, gulls and other colonial species.

Although across taxon associations have been investigated in contexts of indicator species or concordance (Kati et al., 2004; Padial et al., 2012; Paszkowski and Tonn, 2000), species synergies/conflicts in wetlands created to facilitate multiple taxonomic groups are seldom investigated, especially not among birds, fish and amphibians. A better understanding of species associations among those three groups might help to discern the potential outcomes of wetland conservation in general, thereby facilitating wetland creation and restoration for greater biodiversity and making conservation investments more efficient. For example, wetlands could be created to jointly target species that have been identified to share positive associations, while negative associations could imply that creating wetlands for both species could be counter-productive for one or the other.

Environmental characteristics also influence the distribution of taxa and may mask associations between them. These can appear to play more important roles in shaping the bird and fish assemblages than biotic interactions (Paszkowski and Tonn, 2000). Thus, the strength of associations among the three taxa resulting from environmental influences and trophic interactions may be variable. Statistical tools, such as joint species distribution models (see below), can help to account for measured abiotic factors that influence species occurrence patterns and thus observed co-occurrences (Ovaskainen et al., 2017), but such tools are relatively new and thus not widely applied in the published research.

Here we investigate species associations among birds, amphibians and fish in created wetlands. We inventoried bird adult pair and chick abundance, as well as fish and amphibian occurrences in 52 created wetlands in Sweden that were primarily created to benefit bird diversity. We used a joint species distribution model (Tikhonov et al., 2020) to investigate associations among species. These models allow one to partly account for habitat preferences through measured covariates that might otherwise mask more subtle associations due to species interactions or unknown habitat variables. We particularly focus on the associations of the bird community (juvenile and adult birds) with amphibians and fish, as associations between amphibians and fish have been addressed in a previous study (Kačergytė et al., 2021b). Here we present and compare species-species associations while accounting or not accounting for basic measured species-habitat relationships. Assuming adaptive ideal habitat selection by birds, we expected positive species-species relationships between piscivorous bird species and fish and possibly negative associations between non-piscivorous birds and fish species due to potential competition for food and/or predation by fish on bird chicks (for general food preferences of each species, see Table S1). Bird relationships to amphibians were mainly expected to be neutral or positive as several bird species include adult amphibians and their tadpoles in their diet, which could cause birds to be attracted to the wetlands.

## 2. Methods

### 2.1. Study sites and environmental data

In 2018, we surveyed 52 created biodiversity wetlands for bird, fish and amphibian communities in the Uppland region, central Sweden. Species in the region were free to colonise the wetlands after creation, and some may have been introduced (see discussion regarding fish and mallard introduction, Kačergytė et al., 2021b; Söderquist et al., 2021). Some wetlands were created anew, while others were created at sites where a wetland had been drained and converted into a production forest or arable land >50 years ago. The created wetlands were permanent and generally shallow (< 5 m deep) and varied in size (0.5 to 20 ha), age since creation (5–28 years), local habitat characteristics (e.g. amount of water vegetation, connectivity) and habitat characteristics of the surrounding landscape (from forested to open landscapes). We used four local and landscape variables that in previous analyses clearly associated with at least two of the bird abundance and reproductive success indices and with fish and amphibian species occurrences (for details, see Kačergytė et al., 2021a, 2021b that used the same datasets). These were: i) size: wetland size (0.53–19.98 ha), ii) water vegetation: proportion of the wetland covered by emergent and floating water vegetation (e.g. water lilies *Nymphaea*, reed *Phragmites*, cattails *Typha*, duckweed *Lemnoideae*, etc., range = 0–98 %); iii) connectivity: the presence of either or both inflow and outflow, connecting the wetland to other wetlands (28 connected, 24 isolated assuming no temporary connectivity by inundation; see Kačergytė et al., 2021b) and iv) landscape forest: landscape composition estimated as the proportion of forest within 1 km surrounding the waterbody shoreline of the wetland (range = 1–100 % forest). This buffer distance was chosen because previously we found associations with species of birds and fish with the forest within 1 km landscape (Kačergytė et al., 2021a, 2021b). Naturally, there are likely other environmental factors influencing the presence and abundance of aquatic organisms (e.g. water quality and fluctuations) which may explain why species-species relationships accounting for investigated habitat associations still may reflect effects of unmeasured species-habitat associations. Age since creation was not clearly related to occurrences of fish or abundance and reproductive performance of birds (see Kačergytė et al., 2021a, 2021b) and were excluded from following analyses. Habitat variables were estimated from field observations or extracted from topographic maps (<https://geolex.lantmateriet.se/>), land-use (GSD Geografiska Sverigedata) and hand-digitalised maps using ArcGIS software (v. 10.5).

### 2.2. Bird surveys

We surveyed the wetlands between mid-May-early-July in 2018. The inventories were done as transect counts while walking around the wetland at 10 min/ha pace to distribute the effort equally for wetlands of different sizes, surveying the whole water body and the shore. All wetland birds (except passerines) were recorded when observed within the wetland and 50 m around the wetland shore. We surveyed 23 wetland bird species, including ducks, grebes, gulls, geese, swans, terns and rallids (excluding waders and passerines as they do not use open water *per se*). We used audio playbacks for the three most cryptic species (moorhen *Gallinula chloropus*, water rail *Rallus aquaticus* and little grebe *Tachybaptus ruficollis*; see Kačergytė et al., 2021a). Adult pair abundance was estimated by two surveys in the second half of May, primarily following Koskimies and Väisänen (1991) and Petterson and Landgren (2016) methods. We estimated pair abundance as the largest pair abundance count out of the two inventories for each species and wetland during these May surveys. We surveyed the wetlands two more times between the 18th of June and the 3rd of July to estimate the reproductive success of wetland birds, where the number of chicks was counted for each species. Chick abundance was estimated as the largest count of the two surveys for each species/wetland. For more detailed

methods on bird surveys, see Kačergytė et al. (2021a).

### 2.3. Fish and amphibian surveys

Using environmental DNA metabarcoding (eDNA), we determined fish and amphibian presence in water samples. Every wetland was sampled once between June and August 2018. Each sample consisted of a blend of 10 subsamples which were spatially equally distributed (Harper et al., 2019). The collected subsamples were filtered twice through 5 µm glass fibre and 0,8 µm Polyethersulfone membranes (NatureMetrics Ltd., UK) and fixed with 96 % molecular grade ethanol (Spens et al., 2017). The eDNA was extracted in the laboratory (MoRe Research AB, Sweden) using Spens et al. (2017) protocol. The PCR, high-throughput sequencing and bioinformatics of extracted DNA samples were executed commercially (NatureMetrics Ltd). MiFish 12S primers (Miya et al., 2015, 2020) were used for replicating fish DNA, while adjusted MiFish primers were used for amphibians to match them to the 12S region. After bioinformatics processing, the retrieved information of the species list and number of reads was used to construct a species list of five amphibians and 18 fish species. We assumed a species to be present in a wetland if we could detect any eDNA of that species, as eDNA from connected water bodies is less likely to be present due to diffusion distance and degradation of eDNA (Taberlet et al., 2018). For more detailed eDNA laboratory and bioinformatics processing, see Kačergytė et al. (2021b).

### 2.4. Statistical analyses

#### 2.4.1. Structure of models

We used joint species distribution models implemented in the R-package HMSC (Hierarchical Modelling of Species Communities, Tikhonov et al., 2020) to infer species co-variation between bird abundance, fish and amphibian occurrences, and environmental relationships. We used two models combining data on two aspects of bird abundance (breeding abundance representing the adult population or chick abundance representing reproduction) with occurrences of fish and amphibian species and a model only considering species richness.

First, we investigated associations among the three taxonomic groups using pair abundance measures for birds ('bird pair abundance model'). For those analyses, we excluded species that occurred in less than ten sites (p. 174, Ovaskainen and Abrego, 2020), leaving 14 bird, five amphibian and seven fish species for the analyses (26 species in total, Table S1). Second, we also investigated associations among the three groups using chick abundance measures for birds (as a measure of reproductive output, 'bird chick abundance model'). The use of reproductive data may reveal otherwise hidden relationships, as chicks might be more sensitive to food availability (e.g. effects of competition with fish) or be directly predated upon by pike, where adults would not have been directly affected. Therefore, similarly to the joint species distribution model of pair abundance, we modelled fish and amphibian occurrence along with chick abundances. We again excluded species with too few observations (<10 observations, Table S1), leaving only the five most common bird species with chicks. Third, in addition to the species-species associations, we estimated associations between species richness of birds, fish and amphibians ('species richness model'), using the HMSC package. The number of all observed species was included in this analysis for the species richness measure (Table S1). This way, we treated species richness as separate 'species' in the model (i.e. three species richness measures: bird richness, fish richness and amphibian richness). Hence, we asked whether the species richness of birds was positively or negatively associated with the richness of either fish or amphibians. In this way, we can also include information about all species rather than only the more common ones (as in the analyses above).

We fitted two variants of each of the three models above: one without environmental variables and one with environmental variables, to infer

how environmental characteristics may influence the estimated associations between taxa. We first estimated associations for the models without any environmental variables. Then, we estimated residual species associations after accounting for the four environmental variables (size, water vegetation, connectivity and landscape forest) added as fixed effect covariates to the models.

All six ( $3 \times 2$ ) models included species- or species richness-specific intercepts and random multivariate association effects independent among sites, but that might be correlated among species (or richness). These association effects are modelled as latent site factors with species-specific loadings within the HMSC package (Ovaskainen and Abrego, 2020). For the three models with environmental variables, separate coefficients were estimated for each species.

Bird pair abundance and chick abundance were modelled using a Poisson log-normal distribution with a log link (due to overdispersion among sites, but that might be correlated among species; for whooper swan *Cygnus Cygnus* only one pair occurred per wetland and we used a Bernoulli distribution with a probit link). Since fish and amphibian occurrences were based on presence-absence data, we used a Bernoulli distribution with a probit link. Fish, amphibian and bird species richness (third set) were modelled with Poisson error distribution and log links. We used the default priors (uninformative/vague) in the HMSC package (see section 8, Ovaskainen and Abrego, 2020) and mean-centred and scaled the environmental variables by their standard deviations. Wetland size was log-transformed to reduce the skewed size distribution towards smaller wetlands. To compare and check whether the exclusion of information on species abundances of birds would make a difference, we also ran additional models using only occurrences for all three taxonomic groups (Appendix 1). For the models using bird pair abundance, we used 10,250,000 iterations. For the models using bird chick abundance, we used 20,250,000 iterations due to convergence issues. We started sampling from iteration 250,000 for the posterior distribution for these models. For the Species richness models, we used 1,125,000 iterations and started sampling from iteration 125,000 for the posterior distribution. We used 2000 samples for estimating the parameters (but 1000 for Species richness models) and two MCMC chains.

#### 2.4.2. Cross-validation

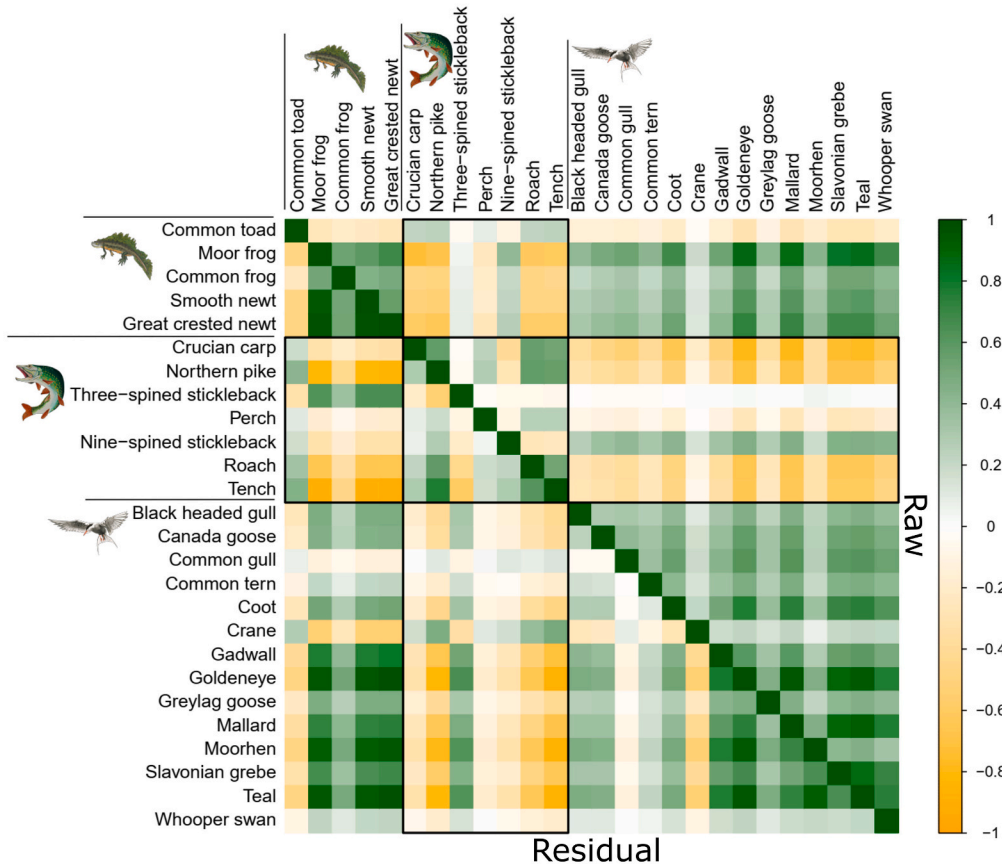
To investigate whether associations among the species groups (rather than species by species) contribute to model performance (predictive power), we also performed conditional and unconditional cross-validation of the two joint species distribution models. First, we used unconditional cross-validation with 10-folds, where data were randomly divided into 10 groups of 5–6 wetlands. After fitting the joint species distribution model for a specific fold (i.e. with one of the groups of 5–6 wetlands withheld), we predicted species occurrences/abundances for each of the 5–6 left out sites and assessed the performance of the prediction. Only environmental variables and model structure was used to predict the occurrences/abundances in unconditional cross-validation, but not information about the presence/abundance of other species. Next, we calculated conditional cross-validation using the same 10 folds as in the unconditional cross-validation, but also splitting the species data into three separate folds, one for each of the groups of amphibians, birds and fish, resulting in a total of 30 folds. In each fold, all the species from one of the groups were withheld from the 5–6 sites when fitting the joint species distribution model. The predictions were then made on this specific group of species at the left-out sites. Thus, in contrast to the unconditional cross-validation, the predictions were informed not only by the environmental predictors at the left-out sites, but also by the presence or abundance of all the species in the two groups that were not withheld. If correlations between species in different groups are strong, this extra information is expected to lead to better predictive performance compared to the unconditional cross-validation. Therefore, the difference in predictive accuracy between the two approaches indicates how much species associations contribute to the joint species distribution model precision (see section 7.7 in Ovaskainen and Abrego, 2020

for more details).

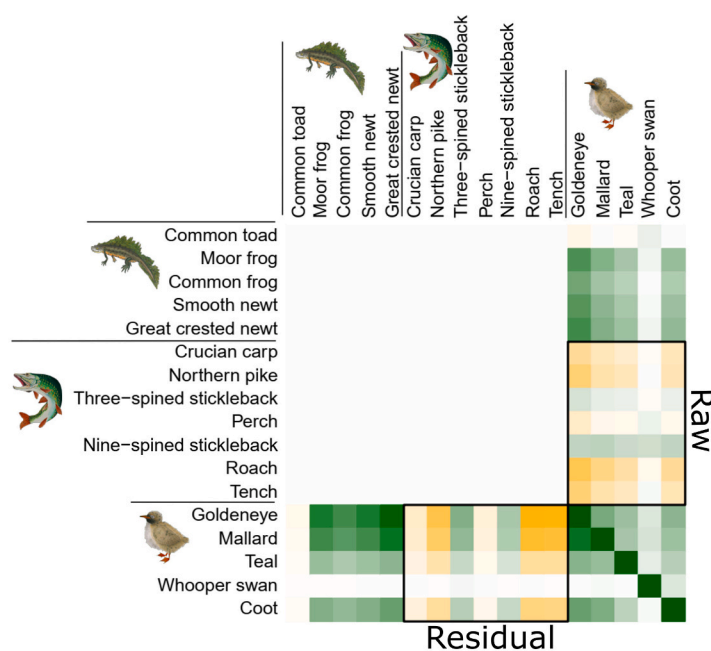
As cross-validation is computationally demanding and time-consuming, we only did this for the bird pair abundance model and bird chick abundance model with environmental variables (see

additional cross-validations for two models, only using chick and adult occurrences instead of abundances, Appendix 1). The model predictive (and explanatory, see results) powers were measured using Tjur  $R^2$  for occurrences (mean predicted probability of presence over presence

### A) Bird pair abundance model



### B) Bird chick abundance model



**Fig. 1.** Species-species associations measured at the wetland level using a model without environmental variables (above diagonal, ‘raw’ association) and a model with environmental variables (wetland size, water vegetation, connectivity and landscape forest; below diagonal, residual associations) using joint species distribution models (HMSC R package). The models are fitted to data on **occurrence** for amphibians and fish and **abundance** data for birds. A) Bird pair abundance model and B) Bird chick abundance model. The coloured squares indicate the estimated species-species association parameter values (correlations at the scale of the linear predictors) as labelled by the scale, either positive (green 0–1) or negative (brown –1 - 0). Amphibian-fish associations in B panel were excluded as they were similar to the A but can be seen in Table S3. The posterior probabilities can be seen in Figs. S4–5 and Tables S2-S3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

points subtracted by mean predicted absence probability over absence points) and pseudo- $R^2$  for abundances ( $SR^2$ , based on Spearman rank correlations between fitted and observed values, Tikhonov et al., 2020). The values range between 0 and 1, where one would mean an outcome where all predictions matched the data perfectly (100 %), while 0 would mean a very poor match. In the case of negative values, the model predictions are opposite to observed values.

### 2.4.3. NMDS

Finally, to visualise the whole community composition (i.e. using all species) and potential overlap between species, we ordered species and sites using non-metric multidimensional scaling (NMDS) along three dimensions, measured as species dissimilarity (see Appendix 2 for more details).

All analyses were done using R 4.0.4 software (R Core Team, 2021).

## 3. Results

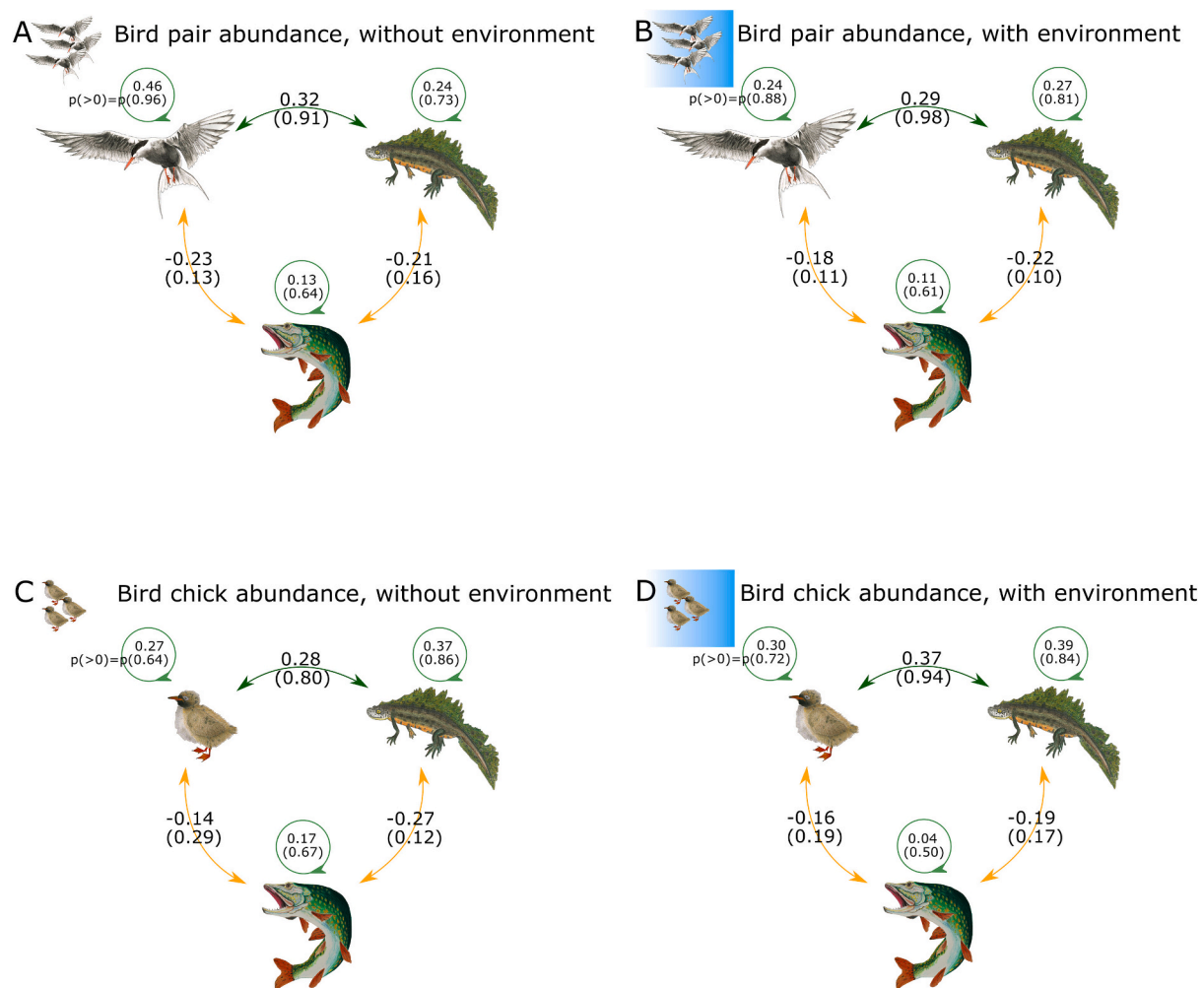
### 3.1. Environmental associations

The three models (bird pair abundance, chick abundance and species

richness) with environmental variables (i.e. including the four fixed effects) showed that most species and species richness were associated with the investigated environmental variables (Figs. S1 for species-species models; Fig. S2a for Species richness model), as previously demonstrated (Kačergytė et al., 2021a, 2021b). The bird pair abundance model explained, on average, 20 % of the variation in the occurrence of amphibians and fish (Tjur  $R^2$ ) and 23 % of the variation in bird pair abundance (pseudo- $R^2$ ). On average, the bird chick abundance model explained 16 % of amphibian and fish occurrence and 36 % of bird chick abundance variation. Out of the variance explained by the three models on average across species, 80 % was attributed to environmental covariates, and 20 % to among species associations (at the linear predictor scale, Figs. S2b, S3). Hence, the residual variation representing species associations was relatively low.

### 3.2. Patterns of species-species associations

In general, bird pair abundance (Fig. 1a) or bird chick abundance models (Fig. 1b), with and without environmental variables, showed similar broad patterns of associations between the three taxa but with uncertain estimates for most species pairs (posterior probabilities of a



**Fig. 2.** Mean amphibian-fish-bird between or within-group association estimates (green arrows for positive and yellow arrows for negative estimates) measured as the average association parameter values across all species pairs, extracted from bird pair (A-B) and chick (C-D) abundance models. The posterior probabilities of an averaged positive association are indicated in parenthesis. B and D panels represent models with environmental variables (wetland size, water vegetation, connectivity and landscape forest). A and C panels illustrate models without environmental variables. All mean estimates are from the joint species distribution models described in methods (HMSC R package), only summarised at taxonomic group level. The models are fitted to data on bird pair (A-B) and bird chick abundances (C-D), and occurrences of amphibians and fish across all models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

positive association often lay between 0.05 and 0.95). Including environmental correlates in the model, thus accounting for basic environmental relationships, did not reduce the strength of the associations (Fig. 1).

Point estimates of the association between birds and amphibians (posterior means of correlations at the scale of the linear predictors) were generally positive (Figs. 1, S4, Table S2, see Fig. 2 for mean bird-amphibian-fish group associations from the same models). This pattern was consistent across all the models, i.e. analysing either bird pairs or chicks and including or excluding environmental data (see below and Fig. 2, see also Appendix 1). In comparison, associations between birds and fish were generally negative, consistent across all the models (Figs. 1-2, S4-5, Tables S2-S3).

Associations between species *within* birds (both for pair and chick abundance) were generally positive, as were estimates of associations between species *within* amphibians (Figs. 1-2, S4-S5, Tables S2-3), as previously shown with other statistical methods (Kačergytė et al., 2021b). Associations between fish species were more heterogeneous, and the general effects were indistinguishable from zero effect (Figs. 1-2, S4-5, Tables S2-3).

### 3.3. Species richness

The amphibian-fish-bird species richness analyses yielded no strong support for associations. The correlation between bird and amphibian richness was 0.29 with a posterior probability of a positive association of 0.65 (without environmental predictors: 0.3 with a probability of a positive association equal to 0.67). The estimated association between bird and fish species richness was  $-0.08$  with a 0.46 probability of a positive association ( $-0.09$  with 0.45 probability in the model without environment). Between fish and amphibian richness was  $-0.13$  with a 0.43 probability of a positive association ( $-0.12$ ; 0.44).

### 3.4. Cross-validation

The unconditional cross-validation showed generally low predictive power (Table 1), but including information on species abundance (birds) or occurrence (amphibians and fish) improved model predictions for species distributions. The predictive accuracy (i.e. the match between raw and predicted values) increased 20–90 % for amphibians and fish occurrences and about 7–8 % for bird abundances when using the information on the other taxa in the models (i.e. conditional cross-validation, Table 1).

Results were broadly similar when running additional models using only occurrences for all three taxonomic groups. The information reduction from bird pair and chick abundances to only occurrences caused several estimates, especially between bird-species associations, to appear weaker (Appendix 1).

**Table 1**

The unconditional and conditional 10-fold cross-validation results of bird pair and chick abundance models to predict bird abundance and amphibian and fish occurrences separately, along with explanatory power measure. The predictions are presented in the Tjur- $R^2$  measure for species occurrences and SR2 for abundances (can be viewed as pseudo- $R^2$ , only for bird pair and chick abundances). Unconditional cross-validation refers to models predicting species presence/abundance based on species-environment associations. Conditional cross-validation refers to species presence/abundance and species-environment associations conditioned on the presence/abundance of species from other taxonomic groups (a fold for amphibians, fish and birds each), which means that predictions are based both on estimated species-environment and species-species associations across taxa. % change indicates the percentage change in mean  $R^2$  values from unconditional to conditional cross-validation.

Model	Test of model fit	Amphibians		Fish		Birds	
		Mean	% change	Mean	% change	Mean	% change
Bird pair abundance	Explanatory power	0.257		0.152		0.229 <sup>a</sup>	
	Predictive power, Unconditional cross-validation	0.025		0.036		0.071 <sup>a</sup>	
	Predictive power, Conditional cross-validation	0.048	92	0.044	22	0.076 <sup>a</sup>	7
Bird chick abundance	Explanatory power	0.165		0.154		0.358	
	Predictive power, Unconditional cross-validation	0.025		0.043		0.107	
	Predictive power, Conditional cross-validation	0.045	80	0.053	23	0.116	8

<sup>a</sup> Numbers exclude whooper swan as it was modelled with binomial distribution, for which estimates of Tjur- $R^2$  was 0.242, 0.176 and 0.174, respectively.

### 3.5. NMDS

In general, there was considerable overlap between the bird, amphibian and fish species (Appendix 2; Fig. B1), although there was a slight separation between the three communities on some dimensions.

## 4. Discussion

Despite community similarity between freshwater organism groups being previously investigated (concordance, Heino, 2002; Paszkowski and Tonn, 2000), the association patterns of birds with amphibians and fish and the potential synergies or conflicts of wetland creation for those taxa have not been addressed. But, such information may be highly relevant for increasing the cost-efficiency of wetland creation for biodiversity conservation. In our study, several general patterns emerged across the three taxa consolidated by the conditional cross-validation and NMDS, even if most associations between specific species pairs were uncertain. First, estimates of bird-amphibian associations were generally positive. Second, bird-fish associations were generally negative. These patterns were broadly similar for pair abundance, chick abundance and species richness models, and with or without accounting for species' environmental preferences.

Several previous studies of bird-fish associations suggest negative associations driven by competition for food or predation and positive associations due to bird piscivory. Birds and fish may compete for invertebrate food, especially so for chicks (experimental: DesGranges and Rodrigue, 1986; Eriksson, 1979; McParland and Paszkowski, 2006; observational: Elmberg et al., 2010; Kloskowski, 2012; Kloskowski and Trembacowski, 2015). Other studies have shown that negative bird-fish associations may be driven by pike predation on chicks (experimental: Dessborn et al., 2011; observational: Elmberg et al., 2010; Paasivaara and Pöysä, 2008), which is potentially reflected by the negative bird chick abundance associations with pike in our study. In contrast to previous studies (Lammens, 1999; Ortubay et al., 2006; Kloskowski, 2012), we found no broad positive associations between piscivorous bird species and fish presence. Although species-species associations were uncertain in our study, our results, together with previous studies, suggest that as a precautionary strategy for constructing future wetlands for ducks, and possibly other water birds, the risk of fish colonisation and introduction should be reduced. However, such a suggestion could create a conflict when wetland creation's main goal is biodiversity and ecosystem services. Birds are supported by conservation initiatives and provide cultural ecosystem services and hunting opportunities. However, fish also provide ecosystem services, including food production or opportunities for recreational fishing. Our results indicate that the same created wetland may not be able to hold diverse communities of both groups of species, thus, the number of ecosystem services provided by multiple groups of species in a wetland might be limited. To avoid

potential conflicts when creating wetlands for bird diversity and, for example, recreational fishing ponds, their creation should be considered separately.

Compared to bird-fish relationships, very little is documented about bird-amphibian interactions and associations. It has been suggested that both bird and amphibian diversity decreases following fish introduction (Ortubay et al., 2006), while wetland management for birds also benefits amphibians (Tozer et al., 2018). Wetland habitats suitable for a high diversity of amphibians (at least anurans) can also rank high for bird species conservation (Jessop et al., 2015), indicating conservation synergies between these two groups. Additionally, it has been demonstrated that bird abundance is positively associated with amphibian larvae abundance in carp fish ponds, although some duck chicks and grebes might predate them (Kloskowski et al., 2010). Bird-amphibian associations, as observed here, were consistently positive across all models, although linked to quite some uncertainty, and amphibians were also largely overlapping bird communities in NMDS analyses. This indicates a potential for wetland creation synergies. The seemingly positive associations could arise due to weak negative bird-amphibian interactions, potential common avoidance of fish species, or species preference for higher quality wetlands, where food availability is vast enough to support the high demands of developing amphibian tadpoles and bird young. On the other hand, bird and amphibian species may have some opposing preferences for habitat, such as the size or the cover of water vegetation (Fig. S1, Kačergytė et al., 2021a, 2021b; Ma et al., 2010; Sebastián-González and Green, 2014; Semlitsch et al., 2015; Shulze et al., 2012) indicating that conservation synergy in wetland creations for birds and amphibians may not be straightforward.

#### 4.1. The use of joint species distribution models and uncertainties

Our data consist of a full survey of the bird, fish and amphibian communities, and in this context, we consider our sample size of 52 wetlands to be fairly large. Yet, our ability to estimate associations between specific species pairs was limited with wide credible intervals, i.e. signs of low power. This is likely a common problem unless sample sizes are very large. The joint species model may, however, still be useful if many associations, each one hard to estimate with precision, together contribute information about species abundance or presence. We believe that conditional cross-validation is currently the best tool to assess this, as one can compare conditional and unconditional model predictability to investigate to what extent model performance improves when information from groups of species is included. Since random species associations form an integral part of latent variable approaches like HMSC, the weak performance of associations in terms of conditional cross-validation would indicate that latent variable models might be overly complex for the data at hand. While predictive performance was generally low, it increased when other taxa were included in conditional cross-validation, suggesting a limited but noticeable improvement from joint modelling. Although computationally demanding, we suggest that more studies should use conditional cross-validation to rigorously assess what benefits joint species models bring (see also Norberg et al., 2019) and under which circumstances they are most useful.

Here we should also mention the caveats of our data for detecting the signals of complex species interactions. The occurrence data of fish and amphibians, sampled over only one year, inherently contain less information than abundance data for describing species distribution patterns (cf. Blanchet et al., 2020). Our analyses endorse this notion, as the association strength was higher when using abundance estimates for birds than only occurrences (see Appendix S1). Including abundance data for all taxa might increase power, as previous studies using fish abundances or biomass have detected negative bird-fish species associations concerning pair and chick abundance (Haas et al., 2007; Väänänen et al., 2012).

An alternative reason for bird-fish associations appearing less clear than elsewhere could have been due to oligotrophic/eutrophic

conditions. Our wetlands are more likely to be affected by nutrient influx compared to previous studies in oligotrophic wetlands (McParland and Paszkowski, 2006; Nummi et al., 2012; Väänänen et al., 2012). Additionally, the fact that only three out of 52 wetlands were fish free may have contributed to the generally weak co-occurrences with fish (cf. Dessborn et al., 2011; Haas et al., 2007). Furthermore, there are inherent differences in how fish was sampled between the studies. EDNA metabarcoding, used in this study, can detect smaller fish species that are often missed by traditional methods (such as gill-nets, see Kačergytė et al., 2021b), making detected species in previous studies biased towards larger species causing the estimated relationships to appear stronger. Therefore, experimental studies, although possibly impractical for community-level experimentation, would shed more light on potential conservation synergies on conflicts than correlational studies.

## 5. Conclusions

Despite uncertainties, particularly at the species-species level, our study provides a starting point for discussing biodiversity synergies and conflicts in freshwater ecosystem creation and restoration. The observed negative fish-bird associations in our study, corroborated by other studies, suggest that bird-fish conflicts should be considered when creating and managing wetlands for biodiversity. On the other hand, conservation measures for the mutual benefit of amphibians and birds should be considered if positive bird-amphibian associations withstand further scrutiny and if specific environmental variables are identified that allow the coexistence of non-obligate avian predators and amphibian prey. We, therefore, suggest that when creating or restoring wetlands targeting birds, it may be beneficial to reduce access for fish (as indicated for amphibians, see Kačergytė et al., 2021b), and that bird and amphibian communities may be jointly facilitated, making the conservation efforts more cost-effective.

### CRedit authorship contribution statement

**Ineta Kačergytė:** Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Jonas Knape:** Methodology, Writing – review & editing. **Michał Żmihorski:** Writing – review & editing, Supervision. **Debora Arlt:** Writing – review & editing, Supervision. **Tomas Pärt:** Conceptualization, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

### 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.

### Data availability

[Bird pair abundance and reproductive success \(Original data\)](#) (Swedish National Data Service)

[Fish and amphibian occurrences \(Original data\)](#) (Swedish National Data Service)

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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.2023.110031>.

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