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Designing for diversity: Wetland ageing and habitat features at multiple scales influence the use of constructed wetlands by breeding waterfowl

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ABSTRACT

Over the past few decades, Europe has made significant efforts to restore and construct wetlands to halt the ongoing habitat and biodiversity losses. These endeavours require considerable time, investment, and effort, making it crucial to ensure that they are highly effective in achieving their objectives, one of which is biodiversity conservation, including waterbirds. We monitored waterfowl communities at 146 constructed wetlands in unprotected landscapes across Finland. We studied the effects of habitat and landscape (at two spatial scales) variables on four breeding waterfowl metrics – species richness, pair abundance, brood abundance, and mean brood size. We also investigated how these metrics vary as wetlands age over time, and depending on gull populations. We found that wetlands with larger perimeters, more islands, and greater gull abundance supported higher species richness and more breeding pairs and broods. However, mean brood size was unexpectedly lower at wetlands with more islands. Pair and brood abundance peaked seven and four years after establishment, respectively, while species richness declined linearly with age. At the local scale (200 m), wetlands surrounded by more peat-associated elements and built-up cover had lower species richness and mean brood size, respectively. Brood abundance was higher in wetlands surrounded by broad-leaved forest at both the local and regional (2 km) scale, while regional marsh cover positively influenced species richness and pair abundance. Such findings provide valuable feedback on wetland construction and restoration projects, helping to ensure that future initiatives can improve their biodiversity conservation outcomes.

1. Introduction

Wetlands are important reservoirs of biodiversity, providing habitats that host a wide range of taxa (Gopal, 2009). Unfortunately, wetlands have been lost globally over the past centuries, with estimates ranging from 21 % to 87 % (Fluet-Chouinard et al., 2023). Subsequently, populations of most waterbird species have declined globally, largely due to habitat loss (Wetlands International, 2010; Kirby et al., 2008). Waterbird populations are also impacted by the deterioration of habitat quality due to reduced food availability (Arzel et al., 2015; Aarif et al., 2021), changes in water chemistry (Holopainen et al., 2024; Aarif et al., 2025), vegetation structure (Nummi et al., 2013), and surrounding habitat (Kačergytė et al., 2021), the introduction of invasive predators (Toivonen et al., 2024), and climate change (Amano et al., 2020), as well as interactions with other species such as gulls, which can enhance breeding success by deterring other predators (Väänänen et al., 2016) but may also simultaneously predate on ducklings (Dwernychuk and Boag, 1972).

Various strategies have been employed to curb the negative impacts of global wetland loss. While many wetlands are now protected under national and international frameworks that recognise their ecological value (Mo and Pandit, 2024), a significant proportion remains unprotected (Reis et al., 2017). Recent initiatives, such as the European Union's law on nature restoration (European Union, 2024), demonstrate increasing support for ecological restoration to improve intervention outcomes. There has been a rapid growth in scientific literature on wetland restoration and creation, an increasingly important method for ecological compensation (Bertolini and da Mosto, 2021). In particular,

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artificial wetlands can compensate habitat loss by supporting biodiversity conservation (Zhang et al., 2020). However, few studies have assessed how well artificial wetlands built for biodiversity conservation perform, and even fewer have investigated metrics related to breeding success (Kačergytė et al., 2021). Additionally, because artificial wetlands are predominantly established in agricultural or urban landscapes, most evaluations of their biodiversity value focus on these contexts, and consequently, studies from forested landscapes remain notably scarce (Oertli, 2018).

The boreal zone is an important breeding region for many Eurasian waterbirds (Williamson et al., 2013). However, the boreal wetlands in Finland have experienced extensive wetland degradation, alongside declines in breeding waterbird populations that vary by species and wetland type (Pöysä et al., 2019a). For instance, waterbird populations have declined at faster rates in eutrophic wetlands than in oligotrophic wetlands over the past few decades (Holopainen et al., 2024). Trends at the guild-level also differ, with the populations of diving ducks and smaller surface-feeding waterbirds decreasing while those of large herbivorous species such as swans and geese are increasing (Pöysä et al., 2019a). These declines are particularly prominent in wetlands located within anthropogenic landscapes, where changes in water chemistry are more severe, having bottom-up effects on breeding waterbirds (Holopainen et al., 2024). Furthermore, predation by invasive alien species, such as the raccoon dog *Nyctereutes procyonoides*, has placed additional pressure on Finnish waterbird populations (Toivonen et al., 2024).

The Natural Resources Institute Finland (Luke) coordinated the monitoring of breeding birds in wetlands constructed or restored as part of various projects. This monitoring formed part of the SOTKA project, which was launched by Finland's Ministry of Agriculture and Forestry in 2020, aiming to curb waterbird diversity loss by creating or restoring wetlands outside protected areas. Using these survey data, our research aims to unravel the main habitat drivers of waterfowl species richness, pair abundance, and breeding success (brood abundance and mean brood size) in these boreal man-made wetlands. While previous studies have compared the effects of different spatial scales for landscape variables on waterbird distribution (Pérez-García et al., 2014), none have examined how spatial scale influences metrics directly representing breeding success, making this a novel aspect of our study. First, we identify which spatial scale of surrounding habitat characteristics (local-scale, 200 m; and regional-scale, 2000 m) is a more important determinant of the waterfowl metrics. Second, we study which wetland-, landscape-, and biotic- characteristics relate to metrics of waterfowl abundance, species richness, and breeding success. Finally, we make use of the wide range of ages of wetlands to study how wetland succession (ageing) affects breeding waterfowl metrics. Most studies examining wetland age effects have treated it as linear (Snell-Rood and Cristol, 2003) or compared discrete periods (Clipp et al., 2017), but none have modelled it as a continuous non-linear association with breeding bird metrics, or considered interactions with landscape context. We hypothesize that, due to habitat creation, the colonization of wetland vegetation and invertebrates, there will first be population increases. This will be followed by a long-term phase of stability or even a decline in bird numbers, due to decreased nutrient availability and/or

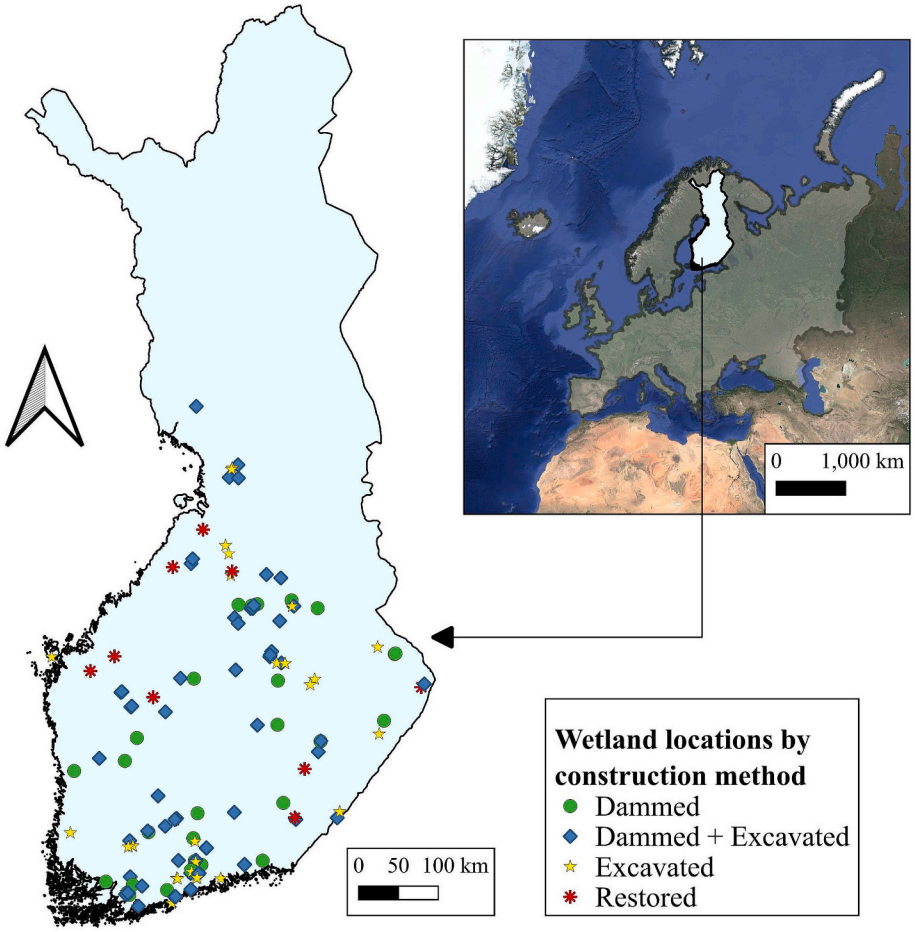

Fig. 1. Locations of the 146 surveyed created/restored wetlands, classified by their construction method: green circles for dammed, blue diamonds for dammed and excavated, yellow stars for excavated, and red asterisks for restored locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

vegetation succession leading to overgrowth. We further hypothesize that successional trajectories will differ depending on surrounding land-use cover and test this using interaction terms.

2. Methods

2.1. Study area and sites

A total of 146 wetlands were surveyed for breeding birds across Finland, ranging in size from 0.04 ha to 86.12 ha (mean = 6.58 ha), with 102 wetlands under 5 ha (Fig. 1). Some of the study sites were recently created, e.g., as part of SOTKA, while others were created during other projects or for other reasons. Most studied wetlands (n = 70) were created using a combination of damming and excavation, while others were constructed through either excavation (38) or damming (29) on previously non-wetland land. The remaining nine wetlands were restored by manipulating natural, typically overgrown wetlands through techniques such as dam construction, water level management, mowing, clearing, and grazing. Surveyed wetlands, constructed or restored between 1980 and 2022 (median = 2012), were primarily located in both forested (mean canopy cover in 200 m and 2 km radius, 52 % and 59 %, respectively) and agricultural landscapes (mean agricultural land in 200 m and 2 km radius, 24 % and 17 %, respectively). Active management, including predator control and the creation of post-breeding staging areas where waterfowl hunting is prohibited, continues in collaboration with local stakeholders and organizations.

2.2. Bird surveys

Between 2020 and 2023, up to three standardized wetland bird surveys per year were conducted at 146 wetlands. Waterfowl were defined as species of Anseriformes order, common coot (*Fulica atra*), common moorhen (*Gallinula chloropus*), and grebes. Surveys included one or two breeding pair surveys during the settlement stage (Round 1: 13 April–31 May (median = 6 May); Round 2: 1 May–28 June (median = 27 May)) to estimate species richness and pair abundance, and a single brood survey during the late reproductive stage (26 June–28 July (median = 6 July)) to estimate brood abundance and mean brood size. The number of surveyed wetlands varied across the years (88 in 2020, 125 in 2021, 133 in 2022, and 79 in 2023). A total of 123 sites were surveyed for both pair and brood surveys in at least two years. Survey methods (round or point count) were selected based on shoreline accessibility, and the mean survey duration was 22.87 min (SD = 14.18), increasing with wetland perimeter (r = 0.4; $p < 0.001$). Recorded data were used to interpret pair abundance for each species during each survey following Koskimies and Väisänen (1991) with minor changes (see Table A1 for details). For each site surveyed in each year, the pair abundance for each species was defined as the higher value of the estimated number of pairs or broods across all surveys in that year. These values were then summed to represent the total pair abundance for that site. Brood abundance was the total number of unique broods counted in the brood survey. A total of 425 wetland-year combinations were used for species richness and pair abundance, and 382 for brood abundance metrics. Brood size was calculated as the mean number of chicks per brood and species, with 785 unique wetland-year-species groupings available for analysis.

2.3. Environmental data and predictor variables

We initially considered eighteen habitat and landscape variables known or hypothesized to influence waterfowl diversity and breeding success (Table A2). A principal component analysis (PCA), correlation matrix, and near-zero variance test (*caret* package; Kuhn, 2008) were used to identify redundancy and variables with insufficient variation, reducing the set to ten final predictors (Table A3, Fig. A1). This final set of predictors was assessed for multicollinearity by calculating variation inflation factors (VIF), and all retained variables had VIF < 2. These included three wetland characteristics (perimeter, islet index, construction method), one biotic variable (gull abundance), five landscape variables (cover of built-up area, broad-leaved forest, marsh area, other wetland shoreline, peat-associated elements) measured at two spatial scales (local 200 m buffer and regional 2000 m buffer), and one temporal variables (wetland age). Three additional variables—an effort variable (included only in species richness and pair abundance models because multiple surveys were used for the calculation of these response variables), a spatial variable (latitude), and a temporal variable (year of survey)—were included to account for potential biases in data collection, amounting to a total of thirteen variables. The selected variables and the rationale for their inclusion are detailed in Table 1, and the collection method is summarized in Table A4.

2.4. Statistical analysis

All analyses were conducted in R (R Core Team, 2023). We used generalized linear mixed models (GLMMs) to assess the effects of predictor variables on species richness, pair abundance, and brood abundance, and linear mixed models (LMMs) for brood size, using the *lme4* package (Bates et al., 2015). GLMMs were fitted with log-link functions using the Poisson distribution (species richness) and negative binomial distributions in cases with overdispersion (pair and brood abundances). LMMs used log-transformed mean brood size as the response. Each response variable was modelled separately at local and regional landscape scales.

All except six explanatory variables (perimeter, age, construction method, gull abundance, year, and effort) were centered on the mean and scaled to unit variance. Perimeter and gull abundance were log transformed, while construction method, year of survey, and effort were categorical variables. Wetland age, which was recalculated for each year of the survey, was modelled both linearly and non-linearly using natural cubic splines (ns) with 3 degrees of freedom (two internal knots placed at the lower and upper terciles), allowing for smooth and flexible estimation of age effects for each response variable and landscape scale. Splines are piecewise polynomial functions joined at specific points, known as knots, ensuring continuity and smoothness across the range of the predictor variable (Perperoglou et al., 2019). We expected a unimodal response of waterfowl metrics to age, modelled flexibly with cubic splines to avoid unnecessary complexity. In case the association of response variables with age was linear, we also treated age as a linear effect in some models (See Table A5). The islet index was converted to numeric midpoints of ordinal categories (e.g., 1–5 islands = 3), which is effective in identifying the inter-category differences (Howard et al., 2014). Site identity was included as a random intercept in all models, while species identity was added as a random effect only in brood size models.

We also explored possible meaningful interactions with age to assess whether wetland succession varied in different landscapes. Interactions of age with built-up, broad-leaved forest, and peatland cover were modelled simultaneously. These variables could influence ecological ageing and thus waterfowl metrics. We defined four candidate models based on alternative treatments of age and potential interaction effects (Table A5). Each response variable was modelled separately at two spatial scales (local and regional), resulting in 8 candidate models.

We selected the most parsimonious model for each response variable and spatial scale using Akaike's information criterion (AIC; Akaike, 1987), fitting all models with maximum likelihood. When the difference in AIC units between competing models was less than 2, we selected the simpler model (i.e., the one with fewer parameters or with linear age) to favor simplicity. We further tested the selected models for zero-inflation (*DHARMa* package; Hartig, 2022) and spatial autocorrelation (Moran's I), and found no substantial evidence for either (Table A6). Landscape cover effects were assessed separately at local and regional scales, and the relative support for each scale was quantified using Akaike weights

Table 1
Predictor variables included in the analyses as fixed effects after an initial selection process. The predictor variables are accompanied by a description, the expected effects on the response variables (number of pairs, species richness, number of broods, brood size), and references to literature supporting the outlined expected effects.

Variable	Description	Expected association and justification	Reference
Wetland characteristics			
Perimeter	Shoreline length in metres, interpreted by using aerial photographs	Positive; widespread studies showing positive species-area relationship	Gonzalez-Gajardo et al., 2009; Arzel et al., 2015
Islet index	Ordinal categories (category 1: 1–5 islets; 2: 6–10; 3: 11–30; 4: > 30)	Positive; islands add safer breeding habitat patches	Burgess and Hirons, 1992; Murray et al., 2013
Construction method	Nominal categories (1: dammed; 2: excavated; 3: a combination of the previous two; 4: restored former lake/pond/bay/wetland)	Restored > Created, Combination > Dammed or excavated; Wetlands with differing construction method will have different succession trajectory	Almeida et al., 2020; Hassett and Steinman, 2022
Landscape cover (both at 200 m (local) and 2 km (regional) scale, estimated buffer distance from wetland shore)			
Built-up area	Urban fabric, commercial and industrial units, linear networks, ports, mineral extraction sites, mines, construction sites, and dump sites, estimated in proportion to the buffer area	Negative; Higher predation and anthropogenic disturbance near urban areas	Avilova, 2023; Dykstra et al., 2024
Broad-leaved forest	Broad-leaved canopy cover, estimated in the proportion of the buffer area	Positive/negative; Effect of forest cover around wetland is species-specific, and can be related to increased predation but also nesting opportunities community metrics	Nummi et al., 2013; Arzel et al., 2015; Morissette et al., 2019; Kačergytė et al., 2021
Marsh	Inland and salt marshes, estimated in the proportion of the buffer area	Positive; Marshes increase habitat diversity and amount	Sica et al., 2020
Wetland shoreline	Total shoreline (in metres) of lakes and sea (excludes rivers), excluding the surveyed wetland	Positive; Additional habitat in the landscape adds to overall habitat available	Sica et al., 2020; Rawal et al., 2021
Peat-associated elements	Coniferous, broad-leaved, and mixed forest on peatland; Transitional woodland/shrub (canopy cover 10–30 %) on peatland; Peatbogs and peat production sites, estimated in the proportion of the buffer area	Negative; Peat-dominated wetlands are generally nutriet-poor and acidic, making them less attractive for waterfowl species	Fox et al., 2025
Biotic variable			
Gull abundance	Total pair abundance of gull species (genus *Larus*)	Positive; Black-headed gulls *Chroicocephalus ridibundus* have previously been identified as protector species for waterfowl in Finland	Väänänen et al., 2016
Temporal variable			
Age	Age during the year of the survey from the year of foundation	Non-linear, with an optimum after a few years, then negative; wetlands reach optimum habitats for waterfowl after a few years of succession, before deteriorating in habitat condition as time passes	Comín et al., 2001; Antoniazza et al., 2018
Year	Nominal categories of the year the survey was carried out (2020,2021,2022,2023)	Uncertain; Inter-annual variation is possible likely due to variables unaccounted for	
Effort variable			
Effort	Nominal categories of the number of surveys carried out at a site in a year (1,2,3).	Positive; Accounts for the expected higher metrics in the sites with more surveys	
Spatial variable			
Latitude	Latitude of site in Universal Transverse Mercator (UTM) coordinate system	Negative; Accounts for latitudinal variation in bird metrics, expected lower bird metrics in northern wetlands	Somveille et al., 2013

(wAIC) across candidate models, with marginal R^2 values reported for the best-supported models. Effects of other predictors (wetland, biotic, and temporal) were based on the most parsimonious model across scales. Tukey's post-hoc tests (*emmeans* package; Lenth, 2024) were used to compare bird metrics across construction methods, survey years, and effort. We visualized the effects of significant continuous predictors using the *predictorEffect* function (*effects* package; Fox and Weisberg, 2019) to extract model predictions and 95 % confidence intervals. Where applicable, predictions were back-transformed using the exponential function, and scaled variables were also rescaled to original values for easier interpretation. To estimate uncertainty around age at which pair and brood abundance is maximum, we generated 1000 bootstrap resamples, refit the GLMM to each resample, recomputed the peak age, and derived 95 % percentile confidence intervals from the bootstrap distribution.

3. Results

3.1. Model selection

Across the four response variables at two landscape scales, Model 2

— the base model with a splined effect of wetland age — provided significantly lower AIC in six cases. Only for species richness at the regional scale and brood abundance at the local scale, Model 1 — the base model with a linear effect of age and no interaction terms — was identified as the most parsimonious.

3.2. Local- and regional-scale comparisons

For species richness and pair abundance, models with regional-scale (2 km) landscape variables had lower AIC values than local-scale (200 m) models, received higher total Akaike weights (wAIC = 0.92 and 0.91, respectively), and exhibited slightly higher marginal R^2 (0.32 and 0.48; Table A8). Mean brood size, in contrast, was better explained by local-scale variables (wAIC = 0.93; marginal R^2 = 0.04). Brood abundance showed moderate support for both scales, with a slight preference for regional variables (difference in AIC units for best model at each scale < 2; wAIC = 0.58; marginal R^2 = 0.39). Together, these results suggest that waterfowl settlement and pair formation respond more strongly to broader-scale landscape context, while reproductive output, particularly brood size, is influenced primarily by fine-scale local conditions. Full details of model comparisons, AIC, wAIC, and marginal R^2 for all candidate models are provided in Table A8.

3.3. Effect sizes in best-ranked models

The estimates, standard errors, and *p*-values associated with every variable from the most parsimonious model for both scales and all bird metrics are summarized in Table A9. According to the most parsimonious model for each response variable, wetland perimeter was the only variable that had significant ($p < 0.05$; estimates: species richness = 0.33 ± 0.04, pair abundance = 0.54 ± 0.08, brood abundance = 0.5 ± 0.12) or near-significant ($p < 0.1$; mean brood size = 0.09 ± 0.04) positive associations with all four response variables (Fig. 2, Table A9). Species richness (0.09 ± 0.03), pair abundance (0.13 ± 0.05), and brood abundance (0.17 ± 0.08) increased with increasing islet index, while brood size declined (−0.05 ± 0.03; Fig. 2). Age of the wetland showed a clear negative association on the first spline for pair abundance (−0.69 ± 0.24) and brood abundance (−1.34 ± 0.38), first increasing (marginally for the latter metric) and thereafter peaking and decreasing. Both response variables showed a blunt peak, or optimal age, at 6.7 years (95 % CI: 4.32–8.43 years) for pair abundance and 4.54 years (95 % CI: 1.94–7.78 years) for brood abundance after wetland establishment. Species richness showed a linear decline with age (−0.006 ± 0.004), while brood size did not show any association. All response variables except brood size (estimates: species richness = 0.09 ± 0.02, pair abundance = 0.14 ± 0.03, brood abundance = 0.15 ± 0.04)

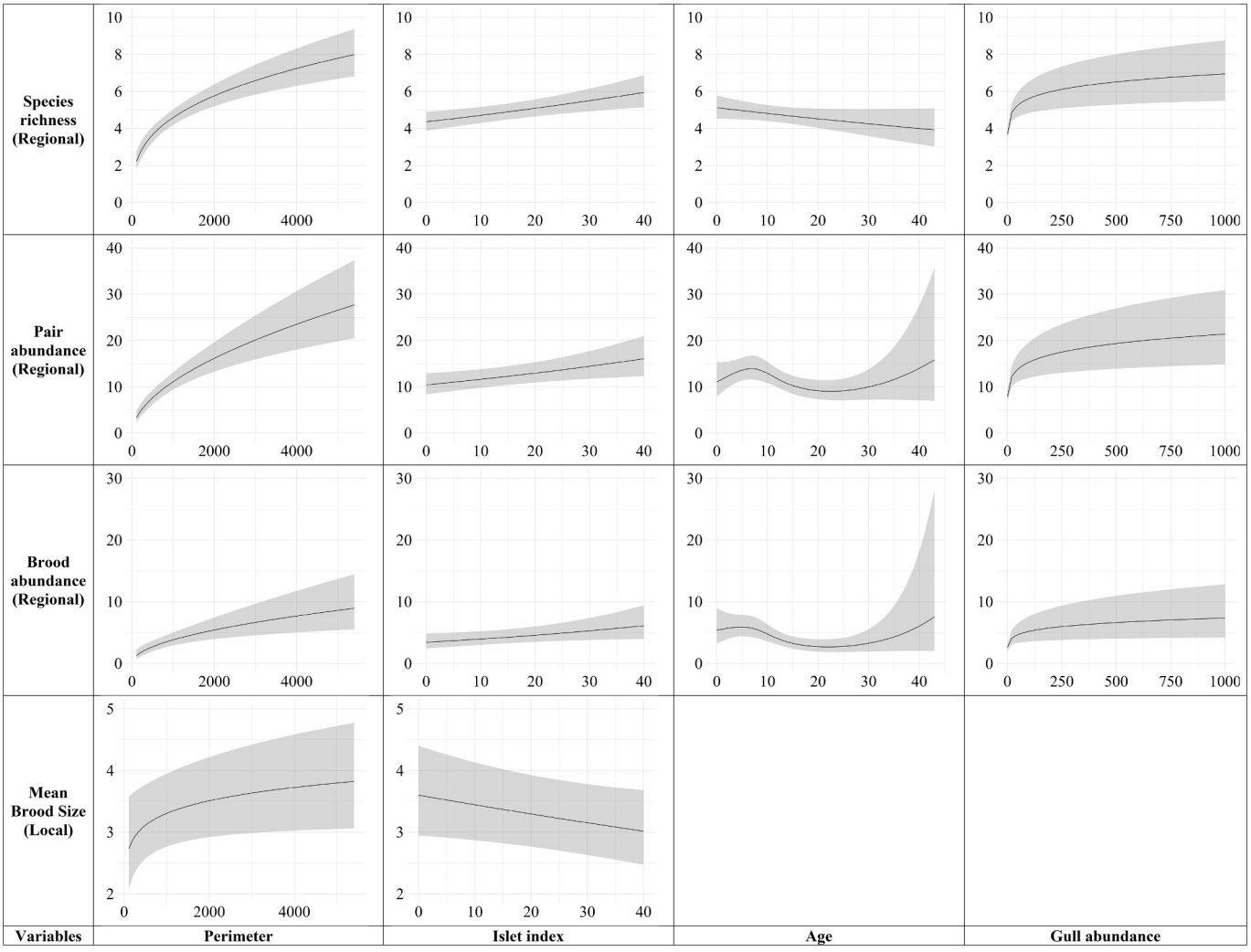

Fig. 2. Predicted significant associations of wetland characteristics, biotic, and temporal variables with the four bird metrics based on the best-ranked model parameter estimates across the two scales (the most parsimonious scale is given in brackets for the bird metrics) with 95 % confidence intervals (CI, shaded areas). The bottom row represents the x-axis labels (the predictor variables), while the first column represents the bird metrics (i.e., response variables; the y-axis label for all plots).

increased with gull pair abundance (Fig. 2). Wetland shoreline and latitude were the only variables with no significant association with any of the bird metrics (Table A9). More surveys corresponded to higher bird metrics, but there was no difference between wetlands with different construction methods and across the year of survey (Table A9).

According to the best models at the local scale, built-up, peat, and broad-leaved forest cover showed significant associations with one or more response variables (Fig. 3). Species richness (−0.08 ± 0.04) and mean brood size (−0.06 ± 0.03) were lower in wetlands with a higher cover of peat-associated elements and built-up area in the local landscape scale. Meanwhile, brood abundance increased with higher broad-leaved forest cover at both the local (0.21 ± 0.09) and regional scale (0.18 ± 0.08). Marsh cover at the regional scale showed a positive association with both species richness (0.07 ± 0.03) and pair abundance (0.1 ± 0.05). (Fig. 3, Table A10).

4. Discussion

Constructed and restored wetlands are capable of supporting significant waterbird diversity (Anderson and Rooney, 2019; Kačergytė et al., 2021; Table A7). Given the high costs associated with wetland construction, restoration, and maintenance, it is crucial to maximize the ecological output of these wetlands (Lethbridge et al., 2010). The results of this study provide information on the importance of scale and various biotic and abiotic factors in improving different metrics of waterfowl communities at constructed and restored wetlands in Finland. This information is important not only for the ongoing management of these wetlands to improve waterfowl diversity and reproduction, but also for future wetland projects with similar objectives.

4.1. The importance of spatial scale

Breeding habitat selection by birds is inherently scale-dependent (Mayor et al., 2009). In this study, settlement-phase metrics were better explained by variables at the regional scale, while mean brood size responded more strongly to the local scale. According to Johnson's (1980) hierarchical model selection, waterfowl likely identify potential breeding sites on a broader scale during the settlement phase, before selecting optimal sites on a finer scale for breeding (Jedlikowski et al., 2016). Mechanisms behind this initial settlement phase are poorly understood, but are believed to be driven by food availability in the broader landscape (Eichholz and Elmberg, 2014). Meanwhile, the fine-scale selection during the breeding stage is likely a balancing act between food availability and predator avoidance (Bloom et al., 2013). In Finland, for example, ducks have been observed shifting to increasingly lush sites as the breeding season progresses, likely driven by the need for better feeding opportunities after hatching (Nummi and Pöysä, 1993). However, while one scale may dominate for certain processes, multiple variables likely interact across scales to shape waterbird communities (Sica et al., 2020; Kačergytė et al., 2021). Future studies that assess breeding success in relation to food availability and predation risks at different scales will be needed to entangle the scale-dependent site selection process in waterfowl.

4.2. Site-level variables

Positive species–area relationships are well established for wetland bird communities (Gonzalez-Gajardo et al., 2009; Arzel et al., 2015). Consistent with this, all bird metrics in this study increased with wetland perimeter. This likely reflects greater habitat availability in larger wetlands, though not all species prefer shoreline habitats (Holopainen et al., 2015). The positive link between perimeter and brood size is less well understood, but a similar pattern was reported in Swedish constructed wetlands, where chick abundance increased with wetland size (Kačergytė et al., 2021). Further research investigating this association will be needed, as it may not be consistent across species and guilds (Holopainen et al., 2015).

Islands are widely recognized as valuable wetland features, offering roosting, nesting, and shelter opportunities for waterbirds (Burgess and Hirons, 1992), primarily by reducing risks from mammal predators and human disturbance along shorelines (Murray et al., 2013). In Finland, invasive predators like Raccoon Dogs and American Mink, alongside natural predators, threaten waterbirds (Pöysä et al., 2023; Selonen et al., 2024). As expected, species richness, pair abundance, and brood

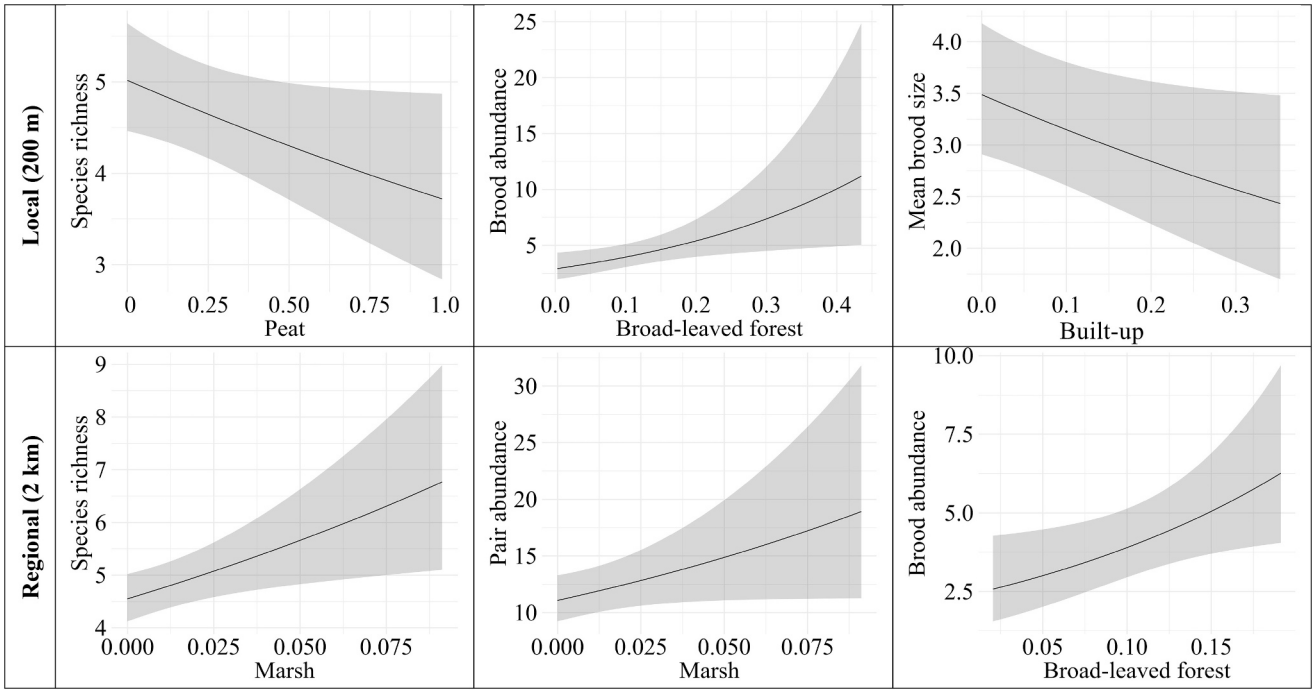

Fig. 3. Predicted significant association of landscape variables at the local (200 m) and regional (2 km) scale with the four bird metrics based on the best model coefficients (shaded areas indicate 95 % CI).

numbers increased with island numbers. Surprisingly, brood size declined with more islands. Broods' preference for islands may give predators a cue in their search for nests. Predators like Raccoon Dogs and American Minks may continue to pose threats to waterbird eggs and chicks due to their swimming capabilities, and islands may be acting as ecological traps (Mulder, 2012; Schwarzer et al., 2016). Moreover, more islands might not necessarily equate to better nesting success. Instead, island configuration might be more important, with fewer small islands that are narrow and elongated being better at attracting waterbirds (Hartman et al., 2016). Future research should take into account the configuration of islands in addition to their numbers to entangle the complete waterbird-island association and maximize their potential.

Waterbird community dynamics and associated diversity metrics change over time with vegetation succession (Comín et al., 2001), the purpose of creation (Balcombe et al., 2005), and management interventions (Antoniazza et al., 2018). Most studies treat wetland age effects as linear (Snell-Rood and Cristol, 2003) or compare discrete periods (Clipp et al., 2017), though long-term research suggests non-linear patterns (Antoniazza et al., 2018). The use of splines here revealed non-linear relationships for pair and brood abundance, with both increasing in the early years, likely due to site discovery and vegetation succession (VanRees-Siewert and Dinsmore, 1996; Herremans, 1999). This initial increase is followed by a peak in bird diversity, likely due to bird preference for wetlands of intermediate succession (Comín et al., 2001) or because wetlands reach their carrying capacity. In this study, pair and brood abundance peaked at around seven and four years, respectively. Similar figures of a peak in the bird community around the age of four to six have been observed before (Comín et al., 2001; Antoniazza et al., 2018). This peak can also occur later (Balcombe et al., 2005), or for other community metrics, such as species diversity (Hapner et al., 2011) and functional diversity (Li et al., 2019). While the precise timing of the peak is uncertain, as reflected in the confidence intervals, the overall pattern on an early peak remains robust. After this peak, the numbers gradually declined over the next decade, but it becomes difficult to predict what will happen to the numbers several decades after the creation of wetlands due to the limited number of old wetlands. Previous studies have shown that in significantly older wetlands, waterbird metrics are likely to stabilise in the absence of management (Snell-Rood and Cristol, 2003; Balcombe et al., 2005), given that the water body retains open water. To maintain a high breeding waterfowl diversity, regular renewal of the wetlands may therefore be recommended, e.g., by draining the water for a fallow year or managing the wetland vegetation. Further research into the ecological and physico-chemical processes driving these trends could refine wetland management strategies.

Constructed wetlands are typically poorer habitats for waterbirds than natural or restored wetlands (Snell-Rood and Cristol, 2003; Almeida et al., 2020). Restored wetlands, on the other hand, often match natural ones in bird diversity (Anderson and Rooney, 2019; Almeida et al., 2020). However, our study found no differences in bird metrics between different construction methods or between constructed and restored wetlands. The limited number of restored sites (9/146) may have prevented the detection of true differences. Although combining excavation and damming can improve water quality and potentially alter succession (Hassett and Steinman, 2022), no evidence of differential waterbird responses was observed here. This supports the idea that succession in constructed wetlands generally follows similar trajectories of biotic establishment, driven by spontaneous processes regardless of construction technique (Moreno-Mateos et al., 2015).

According to the protector-species hypothesis, individuals of a species may nest alongside a 'protector' species that responds aggressively to potential threats (Pius and Leberg, 1998). In Finland, black-headed gulls (*Chroicocephalus ridibundus*) are known to be protectors of waterfowl (Väänänen et al., 2016). Consistent with this hypothesis, we find a positive association of species richness, pair abundance, and number of broods with the abundance of gull pairs. However, because our data is observational, it is also possible that gulls preferentially settle in wetlands already rich in waterfowl (conspecific attraction, see Sebastian-Gonzalez et al., 2010). Nevertheless, the positive log-log relationship indicates that even a small gull colony might provide sufficient reproductive success benefit. We suggest that adding suitable habitat for gull nesting could be considered during wetland construction, as the absence of gulls could potentially lead to a decline in waterfowl populations (Pöysä et al., 2019b). Further research is needed to assess the actual predation rates and conditions under which gull colonies benefit wetland birds.

4.3. Landscape variables

There was a clear and fairly strong negative effect of the amount of peatland at the local scale on species richness, but not on the other response variables. The negative association is well in line with the view that many species of waterbirds prefer nutrient-rich and mildly acidic waters over peat-dominated habitats. In particular, Common teal *Anas crecca* is often abundant at even small peat-dominated acidic wetlands (Fox et al., 2025). Teals may be accompanied by a few pairs of Common goldeneye *Bucephala clangula*, and perhaps a pair of Whooper swan *Cygnus cygnus*. Some uncommon species, such as Northern pintail *Anas acuta* or Taiga bean goose *Anser fabalis*, may even prefer these sites, but the general pattern of fewer species on peat-dominated sites is apparent.

Previous studies have reported either negative (Kačergytė et al., 2021; Arzel et al., 2015) or no effects (Nummi et al., 2013) of forest cover on waterbird communities. Unlike these, we specifically examined broad-leaved forest cover and found a positive association with brood abundance at both spatial scales. This contrasts with previous findings from conifer-dominated forests, which could be linked to oligotrophic, food-poor wetlands (Kačergytė et al., 2021). Broad-leaved forests promote higher litter decomposition and likely accelerate wetland eutrophication (Prescott et al., 2000), potentially benefiting broods. Future assessments of the water chemistry of these forested wetlands would be needed to test this hypothesis. Nest predation of Finnish waterfowl is lowest in forested wetlands and highest in agricultural wetlands, which was the second most common land-use type, inversely correlated with forest cover (Fig. A1). This could further explain why broods are larger in wetlands with higher deciduous forest cover (Holopainen et al., 2020).

Marsh-dominated landscapes support greater waterbird diversity (Tourenq et al., 2001), and in line with this, we found that wetlands situated in a region with higher marsh cover supported more species and breeding pairs. Waterfowl are known to prefer landscapes that combine open water with marshes, which provide critical foraging and hiding opportunities (Kaminski and Prince, 1981).

Smaller brood sizes near urban areas have been widely reported in birds (Chamberlain et al. 2008). In waterfowl, studies of tufted ducks *Aythya fuligula* and mallards *Anas platyrhynchos* have shown reduced clutch sizes in built-up landscapes (Avilova, 2023; Dykstra et al., 2024). Similarly, we observed a negative effect of built-up areas on mean brood size, which could reflect increased predation and anthropogenic disturbance associated with urbanized landscapes (Chamberlain et al., 2009; Minias, 2016).

Surprisingly, contrary to our expectations, a greater amount of wetland habitat in the landscape did not translate to higher bird metrics, despite previous studies highlighting its importance (Sica et al., 2020; Rawal et al., 2021). In Finland, where water cover is among the highest globally (UN Environment Programme – processed by Our World in Data, 2025), suitable wetland habitats may not be limiting. As a result, other factors, such as forest and urban cover at the landscape scale or site-level characteristics, may play a more decisive role in site selection. This contrasts with earlier studies conducted in regions where wetland habitats were scarce, and their availability strongly influenced waterbird distributions (Rawal et al., 2021). Moreover, the type of wetlands existing in the landscape, rather than their absolute amount, might be more important (Bloom et al., 2013). We also did not detect a latitudinal

effect, even though this has previously been reported in Finland, which may reflect that our focal wetlands represent only a limited subset of the broader wetland landscape and thus do not capture large-scale geographic gradients.

Constructed wetlands can effectively complement natural wetlands by providing valuable breeding habitat for waterfowl, particularly in landscapes where natural habitats have declined. However, without ongoing management interventions, their ecological value may diminish over time. Our findings indicate that various landscape features influence waterfowl breeding habitat selection and reproductive success at different spatial scales, underscoring the importance of multi-scale planning when creating new wetlands within the landscape. Certain wetland characteristics, such as a larger perimeter, the presence of islands, presence of protector species, consistently enhance waterfowl richness and reproductive success metrics. Recognizing these patterns provides essential guidance for optimizing the biodiversity outcomes of constructed wetlands. Given the substantial time and resource investments required for wetland creation, our results highlight the importance of thoughtful design and adaptive management to ensure these efforts deliver long-term conservation benefits.

CRediT authorship contribution statement

Prakhar Rawal: Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Toni Laaksonen:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Ineta Kačergytė:** Writing – review & editing, Validation, Methodology. **Tuomas Seimola:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Veli-Matti Väänänen:** Writing – review & editing, Investigation. **Andreas Lindén:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to assist with shortening of the text to within word limit and improving language clarity. After using this tool, the authors reviewed and edited the content as needed and takes full responsibility for the content of the published article.

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.2025.111669.

Data availability

Data will be made available on request.

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