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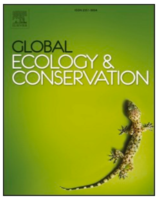

When good turns to bad and alien predators appear: The dynamics of biodiversity change in boreal waterbird communities

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ABSTRACT

Temporal patterns of biodiversity are often difficult to interpret because of our limited understanding of how communities vary through time and how processes drive this variation. A further challenge with dynamic systems is choosing an appropriate baseline against which biodiversity change is judged. We used abundance time series of breeding waterbirds in eutrophic lakes in Finland for 1946–2022 to study the dynamics of biodiversity change in local communities and the relative role of two presumed main drivers, i.e. eutrophication and alien predators, in contributing to historical and recent trends in local abundances and biodiversity. We set the cut-off for the historical and recent study periods in the mid-1980 s, because the systematic monitoring of breeding waterbirds in Finland started in 1986 and recent analyses of biodiversity change and population trends in European boreal waterbird communities are mainly based on time series and data gathered since 1986. Both species richness and the total abundance of waterbirds in local communities showed contrasting trends between historical (gathered before the mid-1980 s) and current (gathered after the mid-1980 s) community time series, with the current time series indicating a decline and the historical time series indicating an increase. The abundances of habitat specialists (species preferring eutrophic lakes) and habitat generalists (species using both eutrophic and oligotrophic lakes) showed a corresponding difference between the current and historical time series. The local extinction rates were higher among habitat specialists than among habitat generalists. The trend indices for wetland-nesting species (highly vulnerable to predation by two alien species (the raccoon dog, *Nyctereutes procyonoides*, and American mink, *Neovison vison*) in terms of nest site) abundances were more negative than the trend indices of species nesting further away from waterbodies (less vulnerable to predation by two alien species). In addition, bottom-feeding species (presumably more sensitive to negative impacts of eutrophication) did not show more negative population trends than surface-feeding species (presumably less sensitive to negative impacts of eutrophication). Regardless of equal sensitivity to negative impacts of eutrophication, two species highly vulnerable to two alien predators showed more negative population trends than a less vulnerable species. The results suggest that increased predation has been an important driver of the population and biodiversity declines in the studied waterbird communities. The mid-1980 s may not provide an ecologically appropriate baseline

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against which changes in the populations and biodiversity of boreal waterbird communities are judged.

1. Introduction

Temporal patterns of biodiversity are difficult to interpret if we have limited understanding of how communities vary through time and how processes drive these variations (Magurran and Dornelas, 2010; Magurran et al., 2010; Dornelas et al., 2013). For example, freshwater biodiversity has declined alarmingly due to multiple stressors, of which pollution and alien species have been proposed to be particularly harmful (Dudgeon et al., 2006; Ormerod et al., 2010; Dudgeon, 2019). However, knowledge concerning the relative role of various stressors and their interactions in driving biodiversity changes in freshwater and other aquatic ecosystems remains limited (Nõges et al., 2016). Similarly, we know little about potential long-term changes influencing the impacts of a particular stressor in each system. A recent analysis combining data from studies across Europe and using various biological response variables for organisms representing both plants and animals revealed that nutrient enrichment (eutrophication) is still the overriding stressor in European lakes (Birk et al., 2020). However, this analysis did not consider biological stressors such as alien species.

While eutrophication unquestionably remains a major stress for freshwater biodiversity, the effects of nutrient enrichment on biodiversity metrics, such as species richness and abundance, may not be linear. For example, when studying the overall relationship between primary productivity and species richness in lake communities, Dodson et al. (2000) found that species richness in five aquatic taxa (phytoplankton, copepods, rotifers, macrophytes, and cladocerans) generally peaked at levels comparable with those of oligotrophic to slightly mesotrophic lakes. Similarly, Penning et al. (2008) showed that the species richness of aquatic macrophytes along a phosphorous gradient peaked at a level corresponding to the mesotrophic situation. The latter authors concluded that the eutrophication of oligotrophic lakes can result in increased species richness, while the eutrophication of natural mesotrophic lakes can result in a decrease in species richness.

Considering temporal patterns of eutrophication, extensive paleolimnological data suggest that conditions before 1850 can be taken to represent reference conditions for lake eutrophication across Europe, although the temporal baseline for individual lakes may vary according to their specific histories and sensitivity to natural and anthropogenic eutrophication (Battarbee et al., 2011; Bennion et al., 2011; Tammelin and Kauppila, 2018). A study using fossil Chironomidae assemblages for a lake in southern Finland revealed a succession from an oligo-mesotrophic (c. 1940–2000) to a eutrophic community (c. 2000–2010) and reaching features of a hypertrophic community during the last years on record (Luoto and Oja, 2014).

Given that lake eutrophication is typically a gradual process and may have continued for centuries, with impacts on biodiversity probably varying through time as suggested by the findings above, defining the reference state for biodiversity change attributable to eutrophication may be challenging; the conclusions reached may change depending on the chosen baseline. This is a general problem in conservation policy (e.g., Bonebrake et al., 2010; Bull et al., 2014; Soga and Gaston, 2018; Collins et al., 2020), including when assessing temporal biodiversity change (e.g., Magurran et al., 2010; Dornelas et al., 2013; Mihoub et al., 2017; Mehrabi and Naidoo, 2022). The case of biodiversity change in boreal waterbird communities in Europe provides a good example. Recent analyses of changes to population sizes and biodiversity in European boreal waterbird communities are based on data gathered since the latter half of the 1980 s (Pöysä et al., 2013; Lehikoinen et al., 2016; Pavón-Jordán et al., 2017; Pöysä et al., 2019a; Elmberg et al., 2020; Holopainen et al., 2022; but see Pöysä and Linkola, 2021 for an exception). A common finding of these analyses is that the breeding numbers of waterbirds have decreased especially in eutrophic lakes, allowing the authors to suggest that habitat degradation due to over-eutrophication has been an important driver of waterbird declines. It is important to note, however, that eutrophication has been considered one of the main drivers of breeding waterbird population increases in Northern Europe since the 1850 s (von Haartman, 1973; Järvinen and Ulfstrand, 1980). This has been largely ignored in the current discussion concerning recent populations and biodiversity declines in European boreal waterbird communities (but see Pöysä and Linkola, 2021). These findings are of great conservation importance because eutrophic boreal lakes have typically had rich bird faunas, with many of these lakes belonging to the Important Bird and Biodiversity Areas in Europe (e.g., Kukkala et al., 2016). Indeed, boreal lakes in Finland harbour considerable proportions of the total European breeding populations of several species (Hagemeijer and Blair, 1997; Keller et al., 2020).

Hence, we are facing a conservation dilemma: how to deal with the impacts of an anthropogenic driver that may have both positive and negative effects on populations and biodiversity in the same system, depending on the state of the process. Considering that eutrophication is a wide-spread and long-lasting process, a fundamental conservation problem is how to determine an ecologically proper baseline against which the eutrophication-driven changes of biodiversity are judged (Mihoub et al., 2017; Cardinale et al., 2018; Rodrigues et al., 2019; Pöysä and Linkola, 2021). This is a particularly challenging question in the biodiversity conservation of European boreal waterbird communities, as the concurrent increase of alien predators may also have contributed to the ongoing declines in breeding numbers and biodiversity in these communities (Pöysä and Linkola, 2021). Indeed, the role of two alien predators, the raccoon dog (*Nyctereutes procyonoides*) and the American mink (*Neovison vison*), in affecting waterbird population declines in eutrophic lakes has been emphasized in recent studies from Finland (Pöysä et al., 2019b; Holopainen et al., 2020a; Holopainen et al., 2021; Pöysä and Linkola, 2021) and elsewhere (Ferreras and Macdonald, 1999; Brzeziński et al., 2020). The first records of these two alien predator species in Finland are from the 1930 s, and since then their numbers have increased strongly until the late 1970 s and beyond (Helle and Kauhala, 1991; Kauhala, 1996; Pöysä and Linkola, 2021). These alien predators may cause long-lasting continuous declines in the breeding numbers of waterbirds, as found in Poland for the American mink (Brzeziński et al., 2020).

Here, we used waterbird abundance data from eutrophic lakes in Finland over eight decades (1940–2020) to study the dynamics of biodiversity change in local communities and the relative importance of eutrophication and alien predators in contributing to long-term trends in species breeding abundances. Our study had two main aims. First, we studied whether differences exist in the biodiversity change of local communities between historical and current data, i.e., approximately between the periods before and after the mid-1980 s. We set the cut-off in the mid-1980 s, because the systematic monitoring of breeding waterbirds in Finland started in 1986 and recent analyses of biodiversity change and population trends in European boreal waterbird communities are mainly based on time series and data gathered since 1986 (see above). Related to this question, and to increase our understanding of how species differing in habitat specialization respond to impacts caused by eutrophication, we also studied whether differences occur in abundance trend patterns between habitat specialists (i.e., species that prefer eutrophic lakes) and generalists (i.e., species that occur in many types of lakes ranging from oligotrophic to eutrophic) (cf. Lehikoinen et al., 2016). Furthermore, to gain a deeper insight into the recent biodiversity changes in boreal waterbird communities (Pöysä et al., 2019a; Elmberg et al., 2020; Pöysä and Linkola, 2021), we also studied the extinction and colonization dynamics by comparing local extinction rates between habitat specialists and generalists. Second, because of the uncertainty regarding whether current population declines in European boreal waterbird communities are driven by eutrophication or by alien predators (see above), we compared the population trends of species breeding in the same local communities but differing in their feeding and nesting ecologies. We tested the following hypotheses. Previous studies have indicated that species nesting in a wetland or near a shoreline are more vulnerable to predation by the two alien predators than species nesting further away from water (Brzeziński et al., 2020; Holopainen et al., 2021; Pöysä and Linkola, 2021). Hence, if increased predation has been the main driver of waterbird population (and, ultimately, biodiversity) declines in eutrophic lakes, we would expect the populations of wetland- and shore-nesting species to show more negative trends than the populations of species nesting further away from water, on the ground, or in cavities. Eutrophication should have negatively affected particularly bottom-feeding species, such as diving ducks, due to overgrowth (less open water for feeding; e.g. Anteau and Afton, 2009; Lehikoinen et al., 2017; Lawniczak-Malińska et al., 2018), increased water turbidity (decreased light penetration, an hence, diminished bottom flora and fauna; e.g. Sand-Jensen et al., 2000; Marklund et al., 2001; Anteau and Afton, 2008), and increased cyprinid fish populations (increased food competition between fish and waterbirds; e.g. Nummi et al., 2016) (see also Hargeby et al., 1994; Anteau and Afton, 2009; Fox et al., 2019). Overgrowth and increased water turbidity should also decrease feeding conditions for pursuit-feeding waterbirds, such as grebes, that need good visual acuity to locate prey. On the other hand, increased fish populations benefit fish-eating pursuit-feeding species (e.g. Martínez Fernaández et al., 2005; Keller and Korner-Nievergelt, 2019). By contrast, these eutrophication-driven changes in feeding conditions should not be so detrimental to surface-feeding species, such as dabbling ducks and coots, because they prefer feeding in shallow water rich in vegetation and are flexible in the use of feeding methods (Pöysä, 1983a; Pöysä, 1983b). Hence, if eutrophication-driven changes in feeding conditions have been the main driver of waterbird population declines in eutrophic lakes, we would expect the populations of bottom-feeding species to show more negative trends than the populations of surface-feeding species, with pursuit-feeding species being somewhere between. Finally, combining the assumptions regarding changes in feeding conditions with the difference in predation pressure between wetland-nesting and cavity-nesting species due to the two alien predators (see above), we can make the following dual prediction. On the one hand, if eutrophication has been the main driver of population declines, all bottom-feeding diving ducks should have declined at the same rate independent of nest site. On the other hand, if predation due to the two alien predators has been the main driver of population declines, wetland-nesting bottom-feeding diving ducks should have declined more strongly than cavity-nesting bottom-feeding diving ducks.

2. Material and methods

2.1. Study area and data

We used published and unpublished time series of breeding waterbirds in local communities of eutrophic lakes scattered across southern Finland (Supplementary material, Fig. A1 and Table A1). A local community consists of the breeding waterbirds of a single lake. Lake classification into eutrophic was conducted by the same persons who performed the waterbird surveys (see below) and was based on characteristics of emergent vegetation that reflect well the trophic status (phosphorous and nitrogen concentrations) of lakes (Holopainen and Lehikoinen, 2021). We only included time series that (i) covered at least four years (not necessarily consecutive; i.e., the same criterion used by Dornelas et al., 2014 for time series to study biodiversity change in local species assemblages), (ii) were collected by the same person using the same survey methods through time, (iii) the annual data included all the breeding waterbird species in the local community (i.e., population estimates for each species and year; here, waterbirds include divers (Gaviidae), grebes (Podicipedidae), ducks, swans and geese (Anatidae), and the Eurasian coot (*Fulica atra*), belonging to the rails (Rallidae); see Supplementary material, Table A2, for a full list of species), and (iv) no management actions had been conducted at the lake before and during the period covered by the time series. The published time series were from the same sources as in Pöysä (1989); this study analysed geographical gradients in the stability of local communities in Finland and, for that purpose, searched for community time series in the journals of local Finnish ornithological societies and in the game biological journal Suomen Riista (see below and Supplementary material, Table A1).

The unpublished time series were collected by Jukka Kauppinen and the authors of this study (see Supplementary material, Table A1) using the standard waterbird survey methods by Koskimies and Väisänen (1991). We have used some of these time series earlier for other purposes (Pöysä et al., 2016; Pöysä et al., 2019b); here, we updated the time series until 2022. Two surveys were conducted each year to cover both early- and late-breeding species. Pair numbers of early-breeding species were interpreted from the 1st survey and those of late-nesting species from the 2nd survey (Koskimies and Väisänen, 1991). For some communities, 4–6 surveys were conducted each year, and pair number interpretation was based on the mean of two successive surveys, as described in Pöysä

(2019). The number of surveys was higher for some communities, because, in addition to estimating annual breeding numbers, the data from these communities were used to study the dynamics of settling phenology of waterbirds arriving from spring migration (see Pöysä, 2019; Pöysä, 2022).

The published and unpublished community time series (n = 34) together cover a period of over seven decades, from 1946 to 2022. We classified the community time series into historical (n = 7; the last year used in the time series was 1986 or earlier (range from 1951 to 1986)) and current (n = 27; the last year used in the time series was later than 1986 (range from 1996 to 2022)) (Supplementary material, Table A1). 1986 was used as a cut-off because all recent analyses (except Pöysä and Linkola, 2021) of biodiversity change and population trends in European boreal waterbird communities are based on time series and data gathered since 1986 (see Introduction).

2.2. *Diversity and abundance metrics*

We wanted to know whether biodiversity changes in local communities show divergent patterns between the historical and current datasets. To this end, we considered two fundamental and widely used metrics of biodiversity in local communities: species richness (number of species) and total abundance (total number of pairs summed over all species) (e.g., Dornelas et al., 2014; Blowes et al., 2022; Storch et al., 2022). Trends in these indices were calculated for each local community. Additionally, by pooling abundance data separately for habitat specialists (here, species that prefer eutrophic lakes) and habitat generalists (here, all the other species, i.e., species that occur in both eutrophic and oligotrophic lakes and species that prefer oligotrophic lakes; Supplementary material, Table A2), we calculated the trends for these two species groups for each local community. To gain insight into the relative roles of individual species in recent biodiversity changes in local communities, we analysed the extinction and colonization dynamics of individual species in local communities using the current time series. To minimize the effect of stochastic presence/absence variation on these dynamics, we considered the occurrence of a species in the first three and last three years (not necessarily consecutive) for each community. Hence, for each community, a species was considered extinct if it was recorded during any of the first three years but during none of the last three years, while a species was considered new (colonization) if it was not recorded during any of the first three years but was recorded during at least one of the last three years.

We also asked whether species that are differently vulnerable to predation impacts by the two alien species or differently sensitive to the presumed impacts of eutrophication due to their different foraging ecologies show differences in population trends (see Introduction). We classified each species according to how vulnerable its typical nest site is to predation by the two alien species (Supplementary material, Table A2), assuming that species nesting among emergent vegetation in the littoral zone and on the ground near the shoreline (vulnerability categories ‘wetland’ and ‘shore’, respectively) are more vulnerable to the two alien predators than species nesting in tree cavities or on the ground further away from the shoreline (vulnerability category ‘other’) (Pöysä et al., 2019b; Brzeziński et al., 2020; Holopainen et al., 2021; Brzeziński et al., 2022). For each community and year, we pooled the abundance data from the species that belonged to the same vulnerability category and calculated the trend in the pooled abundance for each vulnerability category. Similarly, we classified each species according to its typical feeding method (Supplementary material, Table A2), assuming that ‘bottom-feeding’ species are most sensitive and ‘surface-feeding’ species least sensitive to negative impacts of eutrophication, ‘pursuit-feeding’ species being between these species groups. The feeding ecology category ‘herbivore’ was not considered in this analysis, because there were only two herbivorous species (the whooper swan (*Cygnus cygnus*) and Canada goose (*Branta canadensis*)), with infrequent occurrences and low local abundances (Supplementary material, Table A2 and Table A3). For each community and year, we pooled the abundance data from the species that belonged to the same sensitivity category and calculated the trend in the pooled abundance for each sensitivity category. We asked further whether species that are differently vulnerable to predation impacts by the two alien species, but equally sensitive to the presumed impacts of eutrophication due to their similar foraging ecologies, show differences in recent population trends. To answer this specific question, we focused on three species (the common goldeneye (*Bucephala clangula*), tufted duck (*Aythya fuligula*), and common pochard (*Aythya ferina*)) belonging to the same feeding guild (bottom-feeding diving ducks) and with high overlaps in diet and feeding habitat niches (Cramp and Simmons, 1977; Pöysä, 1983a). These three species differed in terms of vulnerability to predation by the two alien species; the tufted duck and common pochard are highly vulnerable to predation by the raccoon dog and American mink, whereas the common goldeneye, being a hole-nesting species, is not (Pöysä et al., 2019b; Brzeziński et al., 2020; Pöysä and Linkola, 2021). For each community and year, we pooled the abundance data for the tufted duck and common pochard and calculated the trend in the pooled abundance, to be compared with the trend in the common goldeneye abundance.

2.3. *Data quality check*

Quality of time series data used to study biodiversity changes is an important and debated issue (e.g., Gonzalez et al., 2016; Vellend et al., 2017; Cardinale et al., 2018). The historical time series used in this study were from articles published in the journals of local Finnish ornithological societies and in the game biological journal Suomen Riista (data sources are given in Supplementary material, Table A1). The time series were gathered by the authors of the articles to study species composition and abundances of breeding waterbirds in local communities (in a given lake). We confirmed method consistency from the original articles. Most important, for each of the time series, same person performed the bird surveys using the same field methods each year. In other words, the historical time series used here are not opportunistic birdwatching or citizen science data that typically are susceptible to several sources of bias such as differences in observer skill and effort and incomplete reporting (van Strien et al., 2013; Kamp et al., 2016; Horns et al., 2018). All in all, the survey methods and pair number interpretations were basically similar between the historical and current (published and unpublished) time series, as they were based on the seminal work of Linkola (1959); see also Kauppinen (1983). In brief, all waterbirds in the census area are counted, identified by species and sex (in species where sex identification is possible) and different individuals, pairs and groups are written down separately. Interpretation of pair numbers is based on these field observations using species-specific criteria as specified in Koskimies and Väisänen (1991); the criteria are given also in Pöysä and Linkola (2021: Supplementary material, Table A2). Because the comparisons of biodiversity change between historical and current time series were based on community-specific trend indices (see 2.4. Statistical analyses), it was particularly important that consistent methodology was used across the study years for a given community; this was the case for all the communities studied here. In sum, we consider both the historical and current community time series used in this study of high quality and comparable between each other.

While the historical time series were well spaced across the southern part of Finland, some of the current time series were spatially clustered (Supplementary material, Fig. A1), raising concerns of possible impacts of autocorrelation in the data and biases in the analyses. However, the scatter of the trend indices for species richness and total abundance did not indicate spatial autocorrelation (i.e., variation among nearby communities was of about the same magnitude than among communities further away), this being the case also with the abundance trend indices for habitat specialists and habitat generalists (Supplementary material, Fig. A2).

2.4. Statistical analyses

We used parametric correlation to measure the magnitude and sign of the trend (change through time; hereafter, trend index) in the diversity and abundance metrics for each local community and ecological grouping of species (see 2.2. Diversity and abundance metrics). The correlation coefficient, ranging from − 1 to + 1, provides a scale-free and directly comparable index of the magnitude and direction of the relationship between continuous variables, and it has been widely used as an index of effect magnitude in meta-analyses (e.g., Hedges and Olkin, 1985; Nakagawa and Cuthill, 2007). We used the Mann-Whitney U-test to compare the trend indices of species richness and total abundance between the historical and current time series as specified above (before vs. after 1986) and to compare relative extinction rates (the number of cases in which a species was present in the first three years but absent in the last three years divided by the total number of cases in which the species was present in the first three years, with possible values ranging between 0 and 1; see 2.2. Diversity and abundance metrics) between habitat specialists and generalists in the current time series data. We used Wilcoxon's matched-pairs signed-ranks test (i.e., data paired at the local community level) to compare the trend indices of abundances in the current time series between any two predation or eutrophication vulnerability categories, as specified above (see 2.2. Diversity and abundance metrics).

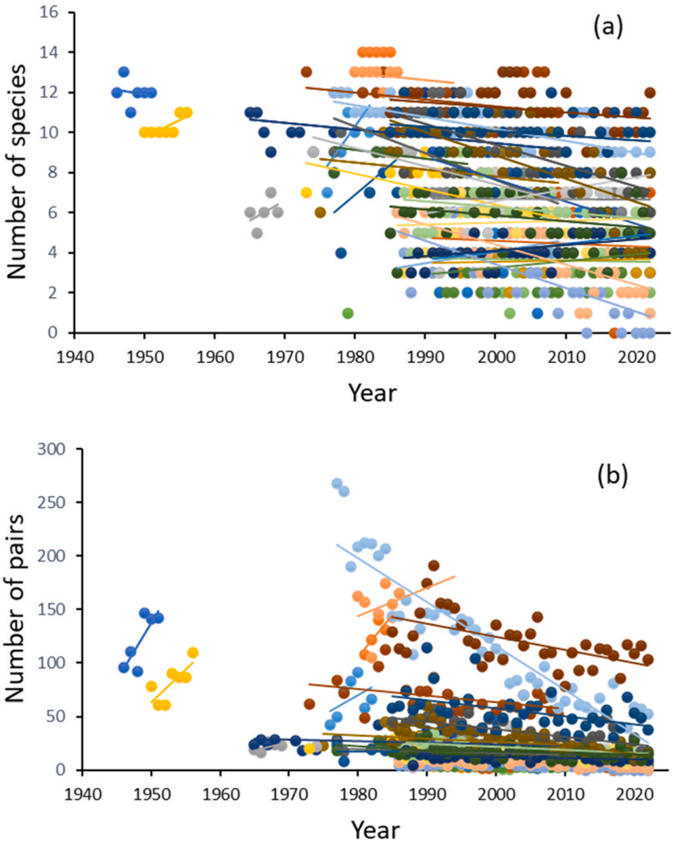

Fig. 1. Raw time series data of species richness (a) and total abundance (b) in local waterbird communities. Trend lines (from linear regressions) are drawn only for illustrative purposes to facilitate the identification of individual communities (n = 34) indicated by different colours.

All reported p-values are for two-tailed tests. Statistical tests were run in SYSTAT 13.

3. Results

3.1. Historical versus current changes in species richness and abundances

Temporal changes (trends) of species richness and total abundance in local communities showed considerable variation across decades (Fig. 1). Community time series length and the number of data points (years) in the community time series also varied greatly among the datasets (see Fig. 1 and Supplementary material, Table A1). However, these did not correlate with the magnitude of the change in species richness (trend index ($|r|$) of species richness versus: time series length, $r = 0.054$, $p = 0.762$, $n = 34$; data points in time series, $r = 0.027$, $p = 0.882$, $n = 34$) or total abundance (trend index ($|r|$) of total abundance versus: time series length, $r = -0.136$, $p = 0.443$, $n = 34$; data points in time series, $r = -0.101$, $p = 0.569$, $n = 34$).

We observed a clear difference between the historical and current time series in the direction (sign) of the trend indices for the community-level measures; both species richness and total abundance showed a positive trend in the historical time series but a negative trend in the current time series (Fig. 2a; species richness, Mann-Whitney U-test, $U = 162$, $p = 0.004$; total abundance, Mann-Whitney U-test, $U = 183$, $p < 0.001$). Similar differences between the historical and current time series were found in the abundance trend indices for habitat specialists (Mann-Whitney U-test, $U = 140$, $p = 0.053$) and habitat generalists (Mann-Whitney U-test, $U = 182$, $p < 0.001$) (Fig. 2b), although the difference was not quite significant for habitat specialists.

3.2. Extinction and colonization dynamics

Considering the current time series, the extinction rate was higher for habitat specialists (mean = 0.490, SD = 0.185, n = 7 species) than for habitat generalists (mean = 0.0.148, SD = 0.149, n = 5 species) (Mann-Whitney U-test, $U = 32$, $p = 0.018$), with the highest extinction rates recorded for the common pochard (0.778), garganey (*Spatula querquedula*) (0.625), pintail (*Anas acuta*) (0.538), and horned grebe (*Podiceps auritus*) (0.538) (Supplementary material, Table A3). The whooper swan was a notable exception to this pattern, as it is a habitat specialist with the highest number of colonization events among all the studied species (Supplementary material, Table A3). The average length of the time periods over which extinction rates were calculated (Supplementary material, Table A3) did not differ between habitat specialists (mean =30.8 years, SD = 1.2, n = 7) and habitat generalists (mean = 30.6 years,

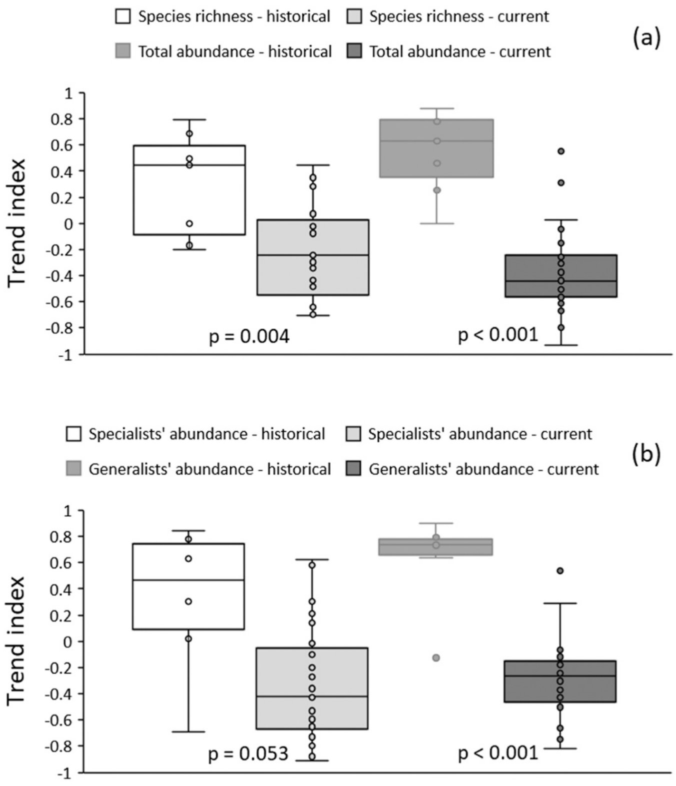

Fig. 2. Box plots for the trend indices of species richness and total abundance (a) and abundances of specialist and generalist species (b) in the historical and current data sets. n = 34 local communities in each case. Statistical significances (p value) for pair-wise comparisons are also given (see the main text for additional information).

SD = 0.1, n = 5) (Mann-Whitney U-test, U = 22, p = 0.460).

3.3. Current abundance trends in relation to vulnerability to impacts caused by alien predators and eutrophication

Current wetland- and shore-nesting species abundances showed more negative trends than those of species nesting further away from waterbodies (other nesters), although the difference between shore versus other nesters was not significant (wetland vs. other, Wilcoxon's matched-pairs signed-ranks test, Z = 2.066, p = 0.039, n = 27; shore vs. other, Wilcoxon's matched-pairs signed-ranks test, Z = 1.734, p = 0.083, n = 23; Fig. 3a). No difference was found between wetland- and shore-nesting species (Wilcoxon's matched-pairs signed-ranks test, Z = 1.794, p = 0.073, n = 23; Fig. 3a).

Abundances of pursuit-feeding species showed more positive trends than those of surface-feeding (Wilcoxon's matched-pairs signed-ranks test, Z = 2.349, p = 0.019, n = 26; Fig. 3b) and bottom-feeding species (Wilcoxon's matched-pairs signed-ranks test,

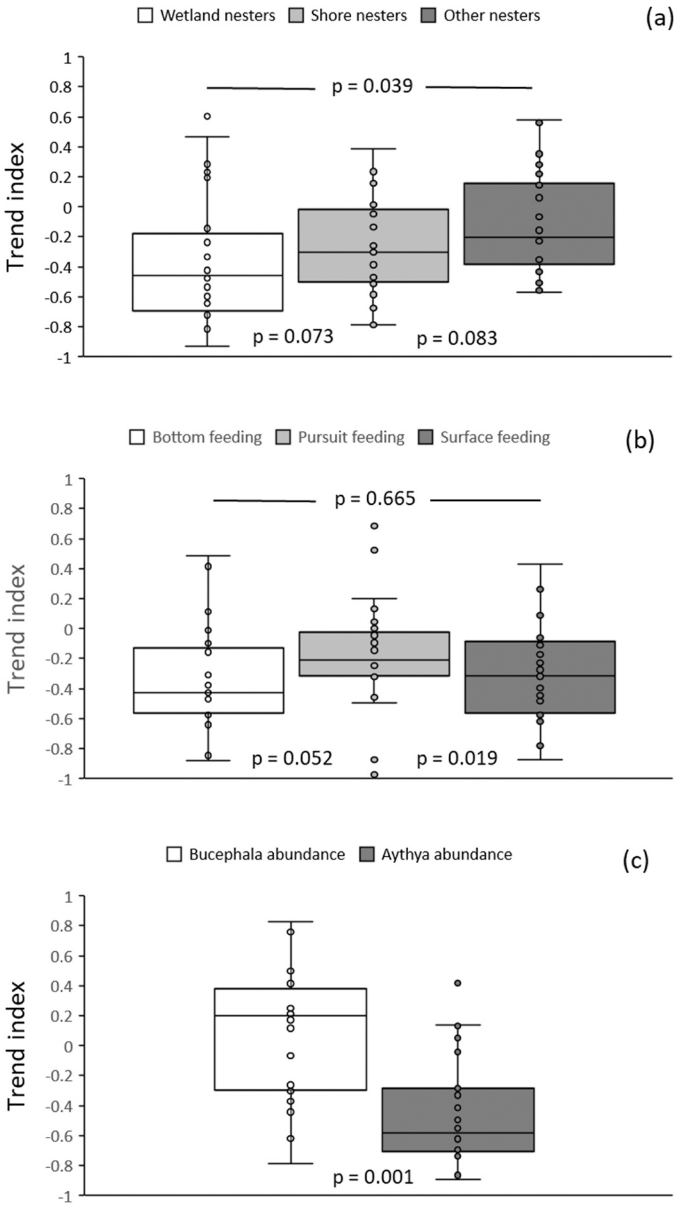

Fig. 3. Box plots for the trend indices of the abundances of wetland nesters, shore nesters, and other nesters (a), bottom feeders, pursuit feeders and surface feeders (b) and of the abundances of common goldeneye (Bucephala) and of tufted duck and common pochard (pooled Aythya) (c) in the current data sets. n = 27 local communities in all cases, except n = 23 local communities for shore nesters and n = 26 local communities for pursuit feeders and Aythya abundance. Statistical significances (p value) for pair-wise comparisons are also given (see the main text for additional information).

Z = 1.943, p = 0.052, n = 26; Fig. 3b), although the latter difference was not quite significant. There was no difference in the trend indices between bottom-feeding and surface-feeding species (Wilcoxon's matched-pairs signed-ranks test, Z = 0.432, p = 0.665, n = 27; Fig. 3b).

We found a clear difference in the trend indices of current abundances within the same communities when considering the three diving duck species that differ in vulnerability to predation by the alien species but not in vulnerability to the impacts of eutrophication (see 2.2. Diversity and abundance metrics); the average abundance of the common goldeneye increased slightly, whereas the pooled abundance of the common pochard and tufted duck decreased (Wilcoxon's matched-pairs signed-ranks test, Z = 3.238, p = 0.001, n = 26; Fig. 3c).

4. Discussion

Our study revealed a clear difference in the change of species richness and total abundance of waterbirds in local communities between historical and current community time series. While the trend indices based on the current time series indicated a decline in these community-level traits, the trend indices based on the historical time series indicated an increase. We found a corresponding difference between the current and historical data in the trend indices of habitat specialist (species preferring eutrophic lakes) and habitat generalist (species that use both eutrophic and oligotrophic lakes) abundances, although the difference was not quite significant for habitat specialists. Related to the current species richness decrease in local communities, the extinction rate was generally higher among habitat specialists than among habitat generalists. Furthermore, we found that the trend indices for wetland-nesting species (highly vulnerable to predation by the two alien species) abundances were more negative than the trend indices of species nesting further away from waterbodies (less vulnerable to predation by the two alien species). In addition, bottom-feeding species (presumably more sensitive to the negative impacts of eutrophication) did not show more negative population trends than surface-feeding species (presumably less sensitive to the negative impacts of eutrophication). These results were complemented by our finding showing that, among three diving duck species equally sensitive to the negative impacts of eutrophication, the abundances of two species highly vulnerable to predation by the alien species showed negative population trends, whereas the species not vulnerable to predation by the alien species showed stable or slightly increasing population trends.

While our results support earlier findings that show breeding populations of species in European boreal waterbird communities to currently be declining, the historical data suggest that the current declines were preceded by strong population increases. Indeed, both the species richness and total abundance of waterbirds in northern European lakes have increased since the 1850 s, with population changes and range expansions having been facilitated by eutrophication and water level decreases in many lakes (Merikallio, 1958; von Haartman, 1973; Järvinen and Ulfstrand, 1980; see Supplementary material, Table A4 and Table A5, for examples). These changes probably are attributable to increases in food supply following eutrophication. The great crested grebe (*Podiceps cristatus*), common pochard, and Eurasian coot have been mentioned as examples of species that historically benefitted from eutrophication and have thus increased in boreal lakes since the 1850 s (von Haartman, 1973). Similar responses of great crested grebe numbers to eutrophication have been reported from southern Europe (Martínez Fernández et al., 2005; Amat and Green, 2010). Interestingly, these species, among other species preferring eutrophic lakes, have decreased and even gone locally extinct in many boreal waterbird communities since the 1980 s (this study; Pöysä and Linkola, 2021). These decadal changes suggest that, after a long-lasting eutrophication process, with initially positive impacts on waterbirds, the impacts of eutrophication have turned negative. Keller and Korner-Nievergelt (2019) also reported on a non-linear effect of eutrophication on the breeding numbers of great crested grebes at Like Sempach, Switzerland. Similarly, based on a cross-sectional study of lakes in southern Sweden, Nilsson (1978) speculated that the eutrophication of formerly oligotrophic lakes will first have positive effects on the density of breeding waterfowl, except species preferring clear water, and will enable new species to appear. However, with increasing eutrophication the waterbird communities will eventually be dominated by a few species (see also Nilsson and Nilsson, 1978). Nilsson (1978) speculated further that, in naturally eutrophic lakes, the nutrient load increase may lead to a poorer waterfowl community, as the important submerged vegetation is destroyed and diving ducks decrease.

Hence, assuming that over-eutrophication has been an important driver of the recent population and biodiversity declines in European boreal waterbird communities, two questions crucial for biodiversity conservation in these communities arise. First, where should we set the temporal baseline for assessing biodiversity change and, second, how can we appropriately target management actions to mitigate the negative impacts of eutrophication on biodiversity? Answering these questions is anything but straightforward. For example, the mid-1980 s, after which waterbird populations in European boreal breeding areas have been systematically monitored and drastic declines have been documented (see references in the Introduction), may not provide an appropriate temporal baseline because, at the time or during the early 1990 s, the populations of many species were obviously at their historical maxima, i.e., at levels probably no longer achievable (see Piha et al., 2022). On the other hand, the biodiversity of boreal waterbird communities is obviously much higher at present than it was in the 1850 s, i.e., the historical reference conditions for lake eutrophication in Europe (see references in the Introduction).

Moreover, even if we could mitigate the negative impacts of eutrophication, it is not at all clear that over-eutrophication has been the main driver of the recent population declines in boreal waterbird communities. Indeed, we found that the increased predation pressure due to the increment of two alien species, rather than eutrophication, has been an important driver of the current population and biodiversity declines in the boreal waterbird communities studied here. It is important to note in this context that those wetland-nesting species that are highly vulnerable to predation by the two alien species and that have declined strongly, differ in both diet and overall foraging ecology; the great-crested grebe is a pursuit-feeding piscivore, the horned grebe a pursuit-feeding invertivore, the common pochard a bottom-feeding omnivore, and the Eurasian coot a surface/bottom-feeding omnivore (Cramp and Simmons, 1977; Pöysä, 1983a). It is difficult to explain the decline of all these species with changes caused by over-eutrophication in feeding conditions alone (see also Pöysä and Linkola, 2021). The whooper swan is an exception among wetland-nesting species, as it is a newcomer in most of the waterbird communities studied here and has colonized many other European boreal waterbird communities in recent decades (Pöysä and Sorjonen, 2000; Pöysä and Linkola, 2021; Holopainen et al., 2022). Considering that the whooper swan is an herbivorous species foraging on submerged aquatic macrophytes, a food resource that has reportedly collapsed due to over-eutrophication (e.g., Sand-Jensen et al., 2000), the colonization of eutrophic lakes by this species suggests that feeding conditions related to submerged vegetation in these lakes are not strongly degraded. The whooper swan has not been affected negatively by the alien predators probably because it is a large territorial species and therefore able to defend its nest and offspring against the alien predators and most other nest predators (see also Pöysä et al., 2019b; Holopainen et al., 2022).

All in all, the results suggest that predation by the two common alien species has been the most important driver of species population declines in the communities we studied. This is in line with findings and conclusions from another recent study, based on different long-term data from southern Finland (Pöysä and Linkola, 2021), and with findings from Poland, where the expansion of the American mink has resulted in population declines of several wetland-nesting waterbird species since the mink's expansion began at the end of the 1970 s (Brzeziński et al., 2020). Similarly, negative effects of the American mink on the density and breeding success of Eurasian coots have been reported from Britain (Ferreras and Macdonald, 1999). The impact of the two alien predators in Finland may even have increased during the last two or three decades, as suggested by the increase in their pooled national hunting bag (Supplementary material, Fig. A3; see also Pöysä and Linkola, 2021). Considering possible native terrestrial predators that could explain recent population trends of waterbirds in Finland, the red fox (*Vulpes vulpes*) is an important potential threat to ground-nesting ducks (Kauhala, 2004) while the pine marten (*Martes martes*) is the most important predator of cavity-nesting species such as the common goldeneye (Pöysä et al., 1997). However, it is unlikely that changes in their numbers can explain population changes of waterbirds in the communities studied here and affect the results of this study, because the hunting bags suggest that red fox has been declining while pine marten has been increasing, with no changes in their pooled hunting bag (Supplementary material, Fig. A3). In addition, recent nest predation experiments with artificial duck nests and wildlife cameras suggest that raccoon dog is a more frequent predator of duck nests than red fox in Finland (Holopainen et al., 2020b). On the other hand, the role of predation in general in driving population declines in boreal eutrophic lakes has probably increased because breeding colonies of the black-headed gull (*Chroicocephalus ridibundus*), which provide efficient protection to other waterbirds against nest predators such as corvids, have disappeared from many lakes (Pöysä et al., 2019b). Nevertheless, over-eutrophication has probably also played a role in the population declines of certain species in some boreal communities (Holopainen et al., submitted manuscript). In more southern areas (southern Sweden and Denmark), waterbirds have been found to respond positively to the recovery of submerged macrophytes and to an increase in macroinvertebrates after phytoplankton blooms have decreased and water clarity has increased (e.g., Hargeby et al., 1994; Hansson et al., 2010; Fox et al., 2019). Some recent analyses suggest that phosphorous and nitrogen concentrations in Finnish lakes show slightly decreasing trends (Holopainen and Lehikoinen, 2021) but, in general, water quality and ecological status of Finnish lakes is still poor (Vilmi et al., 2021). Finally, there have been no changes in hunting regulations in Finland that could explain the differences in population and biodiversity changes between the historical and recent time series. The only exception is the whooper swan that has increased drastically since the 1940 s (e.g. Haapanen, 1987; Pöysä and Sorjonen, 2000; Holopainen et al., 2022), protection from hunting probably being one of the reasons for the increase. In general, hunting pressure has not been found to be an important driver of the recent population declines of waterbirds in Finland (Pöysä et al., 2013).

5. Conclusions and conservation implications

The findings of this study have important general implications to the conservation and management of biodiversity in local communities. In particular, our findings add new insights into the intensively debated issue of whether biodiversity in local communities is declining or not (Gonzalez et al., 2016; Vellend et al., 2017; Cardinale et al., 2018; Primack et al., 2018). In the case communities studied here, the answer is yes and no, depending on whether we consider current or historical time series. This seemingly simple yet equivocal answer reveals two important conservation challenges. First, if an important anthropogenic driver has contrasting effects on biodiversity change depending on the state of the long-lasting impact process, our ability to detect long-term changes in biodiversity may be reduced. This is particularly challenging in systems where the presumed main driver initially has a positive impact on biodiversity but later this impact turns negative, causing a humped pattern of biodiversity through time, as demonstrated here for the impacts of eutrophication in boreal waterbird communities. Vellend et al. (2017) discussed a related problem with the effects of disturbance on the magnitude and direction of biodiversity change. Second, a humped temporal pattern of biodiversity causes another challenge: how to properly determine a temporal baseline against which biodiversity change is judged. Indeed, the problem of setting appropriate baselines against which current biodiversity changes are contrasted has received considerable attention (e.g., Magurran et al., 2010; Bull et al., 2014; Mihoub et al., 2017; Cardinale et al., 2018; Soga and Gaston, 2018; Rodrigues et al., 2019;). This general implication has a direct bearing on decision-making concerning biodiversity conservation in European boreal waterbird communities (see also Pöysä and Linkola, 2021). Specifically, where should we set the temporal baseline against which the degree of the current biodiversity change is assessed? Open discussion among scientists, policy makers, and conservation managers is urgently needed to identify biologically realistic, technically achievable, and societally acceptable conservation targets for biodiversity in European boreal waterbird communities. Furthermore, considering that the strongest declines have been experienced by species highly vulnerable to the impacts of the two alien predators, contributing critically to the biodiversity decrease in waterbird communities of boreal Europe and probably elsewhere, management actions aimed to mitigate the effects of over-eutrophication may not produce desired results if the impact of alien predators is not controlled.

Finally, while we have focused on problems of setting temporal baseline for assessing biodiversity change and on explaining biodiversity changes in local boreal waterbird communities, it is important to keep in mind that these habitats may have other functions that should be considered when setting conservation targets. For example, they may serve as important 'stepping stones' for species moving northwards due to climate warming (e.g., Travers et al., 2021). This may concern not only birds, as exemplified by the historical increases of several avian species in boreal eutrophic lakes (von Haartman, 1973; Järvinen and Ulfstrand, 1980), but also other groups of species dependent on aquatic habitats. Overall, conserving and managing lakes and ponds not as individual sites but as networks of lakes and ponds may be a more effective way to mitigate impacts of anthropogenic pressures on freshwater biodiversity (Hill et al., 2018; Heino et al., 2021; van Rees et al., 2021).

Declaration of Competing Interest

The authors declare no conflicts on interest.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02727.

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