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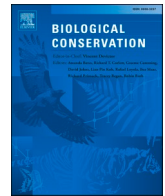
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Policy analysis

Extending temporal baseline increases understanding of biodiversity change in European boreal waterbird communities

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ABSTRACT

Setting relevant temporal baselines is critical to understanding biodiversity change and the full impact of various pressures on biodiversity. Current knowledge of biodiversity change in European boreal waterbird communities is based on monitoring and other data from the last 35 years. However, the impact of the presumed main drivers of changes in these communities, i.e., eutrophication and alien predators, started decades before this. We used data of 35 breeding waterbird communities, representing both oligotrophic and eutrophic lakes, in southern Finland from 1951–1970 and 1996–2015 to study changes in biodiversity against a baseline from a period when the presumed main drivers were not yet fully effective. We found that species richness increased from 1951–1970 to 1996–2015 at oligotrophic lakes but not at eutrophic lakes; total abundance in turn increased at the former lake type but decreased at the latter. Breeding numbers of many historically abundant species declined at the eutrophic lakes to such a degree that the increases of other species were not sufficient to compensate for the declines. Population increases prevailed at the oligotrophic lakes and the slight declines of some previously less abundant species, were compensated for. The species level results revealed that local abundances of different species likely are affected by different drivers, suggesting that we need an autecological approach in the conservation management of boreal waterbird communities. Increased predation risk rather than eutrophication appeared to be the main biodiversity stressor in the waterbird communities studied.

1. Introduction

There is a wide consensus that biodiversity at the global scale is in decline, and we have a good understanding of what the main global drivers impacting biodiversity are (Sage, 2020). However, there are still important issues being debated, such as how to determine a reasonable baseline against which the change of biodiversity is judged (Mihoub et al., 2017; Cardinale et al., 2018; Rodrigues et al., 2019) and how best to measure biodiversity change (Hill et al., 2016; Hillebrand et al., 2018; Primack et al., 2018). Setting the baselines for biodiversity change appropriately is important for several reasons. First, we need to set the baseline appropriately with respect to the action of the presumed main drivers of change to assess their relative importance and understand the full impact of various pressures on biodiversity (Collins et al., 2020). If a presumed environmental driver has begun much earlier than we have been monitoring biodiversity in a particular case, it would be challenging to reliably assess the importance of this particular driver to the

observed biodiversity change. Indeed, as shown by Mihoub et al. (2017), most of the major anthropogenic pressures that are believed to impact biodiversity operated long before biodiversity monitoring schemes were initiated in Europe. Second, due to the shifting baseline syndrome (Pauly, 1995), our expectations of the state of the natural environment may alter. The syndrome arises if each generation of researchers accepts as a baseline the condition of the natural environment that occurred at the beginning of their careers and uses it to evaluate changes; this is likely to result in gradual acceptance of increasingly degraded environmental conditions as a baseline (Pauly, 1995; Soga and Gaston, 2018). Hence, policy makers and resource managers may set inappropriate targets for environmental conservation, restoration and management programs (Bonebrake et al., 2010; Soga and Gaston, 2018). Historical data of species' population sizes are particularly important for judging changes in biodiversity, because abundance itself is among the most important essential biodiversity variables (Schmeller et al., 2018), and data on population abundances provide the most useful basis for

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building various metrics of biodiversity change (Loh et al., 2005; Dornelas et al., 2019).

Similarly, our understanding of how and why biodiversity has changed in a particular case would improve if we study several aspects of biodiversity simultaneously. For example, Hillebrand et al. (2018) showed that the relative magnitude of species richness change in various taxa was orders of magnitude smaller than the actual occurrences of extinctions and immigrations, the latter phenomena leading to substantial turnover not only of rare species, but also in identity and relative abundance of dominant species. Indeed, replacement of species through time without associated changes in species richness appears to be a prevalent form of biodiversity change in local communities across the globe (Blowes et al., 2019; Dornelas et al., 2019).

Here, we address biodiversity change in boreal lake ecosystems, focusing on waterbird communities. Biodiversity in these systems is threatened by multiple stressors, such as climate change, land-use change, eutrophication and invasive alien species (Dudgeon et al., 2006; Heino et al., 2009; Yeung et al., 2019). Waterbirds are an important component of freshwater biodiversity, as they provide important ecosystem services, such as dispersing propagules of many plants and invertebrates, and can be used as bioindicators of the ecological status of aquatic ecosystems (Green and Elmberg, 2014). In addition, waterbirds provide provisioning and cultural services to human in many parts of the world (Green and Elmberg, 2014). Therefore, preserving breeding populations and viable communities of waterbirds would make important contributions to the sustainability of biodiversity in lake ecosystems and also maintain human well-being.

Based on the Finnish waterbird monitoring scheme, established in 1986, boreal waterbird communities show signs of deterioration. Specifically, species and populations associated with eutrophic lakes have been declining while those breeding on oligotrophic lakes are doing better, suggesting that the quality of eutrophic lakes, particularly as a breeding habitat, has decreased (Pöysä et al., 2013; Lehikoinen et al., 2016; Pavón-Jordán et al., 2017). Similar findings have been reported from boreal lakes in Sweden (Elmberg et al., 2020; Pöysä et al., 2019a). Human-caused eutrophication of surface waters and increased rates of nest predation and female mortality particularly due to two alien predators, the American mink (*Neovison vison*) and the raccoon dog (*Nyctereutes procyonoides*), have been suggested among the main reasons for the recent decline of waterbirds in Finland and elsewhere in Europe (Fox et al., 2016; Nummi et al., 2019; Brzeziński et al., 2020). However, it may be questioned whether these drivers can be invoked as general explanations for the recent decline of waterbirds in boreal Europe, because their impact probably started several decades before the population decline of waterbirds was recognized. For example, the anthropogenic eutrophication of surface waters was considered a serious problem in Finland already by the 1960s (Räike et al., 2003; Ekholm and Mitikka, 2006). Similarly, numbers of the two alien predator species had already increased exponentially in Finland by the late 1970s and more or less stabilized after that (Helle and Kauhala, 1991; Kauhala, 1996a). Waterbird numbers reached their lowest point just four years after the mink population reached its highest density in different areas of Poland, although waterbird decline continued up to 15 years after the mink population was established (Brzeziński et al., 2020). Hence, even if excessive eutrophication and alien predators played an important role in the recent waterbird declines in boreal Europe and elsewhere, we may ask whether the late 1980s provides a reasonable baseline for assessing the impact of these drivers.

Here, we use data of breeding waterbird communities in southern Finland from 1951 to 1970 and 1996–2015 to study changes in species richness, abundances and proportional abundances of waterbirds against a temporal baseline (1951–1970) when the presumed main drivers of changes in waterbird abundances were not yet fully effective. Basing on information on the occurrence of aquatic macrophytes and other lake characteristics, we divided the study lakes into oligotrophic and eutrophic (see Section 2.1 Study lakes). While eutrophication may

occur in both lake types, it has been found for boreal lakes in Finland that naturally eutrophic lakes are more sensitive to negative anthropogenic impacts than nutrient-poor, oligotrophic lakes (Tammelin and Kauppila, 2018). Hence, because earlier studies have emphasized the negative impact of eutrophication on waterbird populations in eutrophic lakes (see above), we expected that waterbird communities in eutrophic lakes have changed more than those in oligotrophic lakes.

2. Material and methods

2.1. Study lakes

The waterbird data of this study are from 35 lakes in southern Finland (central coordinate of the study area 61°16'N, 24°17'E; see Supplementary material, Fig. A1, for the location of the study lakes, and Table A1, for additional lake specific information). Hereafter, “lake” and “community” are used interchangeably in the text. A community consists of the breeding waterbirds of a single lake; each of the 35 communities studied here had at least one species in either of the two periods 1951–1970 and 1996–2015. A general description of the study region can be found in Lindholm et al. (2019).

In 1951–1970, P. L. made notes of the occurrence of the most typical aquatic macrophytes (sedges, reeds, herbs and floating-leaved vegetation) and the type of the shore around the lakes. Based on this information, each lake was classified either as oligotrophic (no clear stands of emergent vegetation and little or no floating-leaved vegetation; typically shores with barren moraine and coniferous – pine *Pinus sylvestris* and spruce *Picea abies* – and mixed – pine, spruce and birch *Betula* spp. – forests or narrow belts of poor bog or open fen; $n = 15$ lakes; see lakes ID16, ID28, ID36 and ID44 in Supplementary material, Fig. A2, for examples) or eutrophic (typically surrounded by agricultural land and large stands of emergent vegetation, notably common reed *Phragmites australis* and broadleaf cattail *Typha latifolia*, and open-water areas covered by abundant floating-leaved vegetation; $n = 20$ lakes; see lakes ID1, ID2, ID7 and ID21 in Supplementary material, Fig. A2, for examples). The macrophyte species considered here generally characterize the trophic state of the lakes inhabited by the species (Kolada, 2016; Lawniczak-Malińska and Achtenberg, 2018; Toivonen and Huttunen, 1995). Changes in the main vegetation types have been negligible in the oligotrophic lakes since the 1950s; in other words, these lakes can still be considered oligotrophic. Similarly, eutrophic lakes still have rich aquatic shore vegetation (Supplementary material, Fig. A2). Hence, the relative difference between the oligotrophic and eutrophic lakes in terms of macrophyte luxuriance has remained the same over time, as indicated by the photos taken on 18 July 2020 of some of the study lakes (see Supplementary material, Fig. A2). Although the lake classification is not based on water quality data (e.g. Tot-P, Tot-N, Chl-a), we use the labels “oligotrophic” and “eutrophic” for convenience here. The lakes that were a priori classified oligotrophic are situated at higher elevations (m from sea level; mean \pm SD; 109.9 ± 18.4 , $n = 16$) than the lakes that were classified eutrophic (mean \pm SD; 90.1 ± 7.5 , $n = 20$; elevations derived from the open MapSite service provided by the National Land Survey of Finland, <https://www.maanmittauslaitos.fi>; accessed 29 December 2020) ($t = 4.386$, $df = 34$, $p < 0.001$). This difference gives further support to the relevancy of our lake classification in terms of trophic status, as Lindholm et al. (2019) found in the nearby study area (see above) that lakes high in the landscape are surrounded by coniferous forest and peatlands and have low macrophyte species richness (typical for oligotrophic lakes), while lakes low in the landscape are surrounded by arable lands and human settlements and generally have high macrophyte species richness (typical for eutrophic lakes). Importantly, the qualitative oligotrophic versus eutrophic classification of our study corresponds to that used in Lehikoinen et al. (2016).

2.2. Waterbird surveys

All waterbird data at the 35 study lakes were gathered from 1951 to 1970 and from 1996 to 2015 by one observer (P.L.) using a standard field method (see Pöysä et al., 2019b). Small lakes were surveyed from vantage points or by walking around the lake, i.e., the waterbird point count and round count methods, respectively (Koskimies and Väisänen, 1991). Large lakes were surveyed by rowing in a boat near the shoreline to cover all open water areas. A given lake was surveyed either with the point count or the round count method in all years. Due to logistic reasons, it was not possible to survey all the 35 lakes every year (see below). Some lakes were visited several times in April–May to gather sex ratio data for methodological studies (Linkola, 1959, 1960; Pöysä et al., 2019b), but all species were not surveyed on all visits. We considered only surveys that covered all waterbird species to ensure that the data are representative with respect to all the species constituting a local community (cf. Dornelas et al., 2019). Hence, we included for all lakes and years data from one survey, the timing of which was adjusted annually to take into account the local variation in lake ice phenology (breakup of ice cover). In general, the survey date was earlier in 1996–2015 (mean 7 May, SD = 6 d, n = 231) than in 1951–1970 (mean 11 May, SD = 7 d, n = 101; $t = 4.996$, $df = 330$, $p < 0.001$), the difference reflecting the fact that the timing of ice breakup (affecting the optimal timing of waterbird surveys; e.g. Pöysä, 1996) has become earlier during the last several decades in Finland (Korhonen, 2006; Pöysä, 2019). The Finnish waterbird monitoring scheme recommends two surveys per season, the timing of which varies depending on geographical location (10–15 May and 25–30 May in South and Central Finland, respectively; see also Pöysä, 1996) to also catch late-nesting species, but abundance of each species is estimated using data from only one of the two surveys (Koskimies and Väisänen, 1991). Late-nesting species, too, often settle in the breeding lakes soon after ice breakup (Pöysä, 2019); hence, both early and late species are caught reasonably well in one properly timed survey. The data included for each of the 35 lakes at least one year from both time periods (mean 2.9 years, range 1–9, per lake in 1951–1970 and 6.6 years, range 1–17, per lake in 1996–2015; see Supplementary material, Fig. A3, for the number of lakes surveyed each year by period and lake type).

The waterbird observations from each survey were interpreted as “pair numbers” using the species-specific criteria of Koskimies and Väisänen (1991; summarized in Supplementary material, Table A2). The lake- and species-specific pair numbers were used in subsequent analyses of waterbird abundances and proportional abundances.

2.3. Diversity and abundance metrics

We were interested specifically in changes of waterbird characteristics between the two periods (1951–1970 and 1996–2015) and if the changes differed between the lake types. To that end, we considered the following metrics of biodiversity in local communities: species richness (number of species), total abundance (total number of pairs summed over all species), species-specific abundances and species proportional abundances. For the community-level metrics species richness and total abundance, we used lake- and year-specific data in the analyses (see Section 2.4 Statistical analyses). In the analyses focusing on species-specific abundances and species proportional abundances, we used the mean species- and lake-specific abundances, calculated separately for the two periods using data from all the years a given lake was surveyed (zeroes for each species included). We used the mean species- and lake-specific abundances to also study changes in dominance structure in local communities. We applied the method developed by Hillebrand et al. (2018) to study turnover by changes in species proportional abundances in a community between the two periods as follows:

$$SER_a = \sum_i (p_i - p'_i)^2 / \sum p_i^2 + \sum p_i'^2 - \sum p_i p'_i,$$

where p_i is the proportion of species i in the community in the 1951–1970 data and p'_i is the proportion of species i in the same community in the 1996–2015 data. SER_a approaches 0 if the species identity and dominance structure in a community does not change and 1 if all species are replaced (see Hillebrand et al., 2018). Note that $SER_a = 1$ if the community did not have a single species in either of the two periods (i.e., 1951–1970 or 1996–2015); this was the case for three oligotrophic communities and four eutrophic communities. These cases were included in the final analysis; their exclusion did not qualitatively change the result of the comparison between the oligotrophic and eutrophic lakes (result not shown). Finally, we calculated for each species and community (with occurrence in either period) population change rate: $[\log_{10}(\text{mean abundance in 1996–2015} + 1)] - [\log_{10}(\text{mean abundance in 1951–1970} + 1)]$ (cf. Elmberg et al., 2020).

2.4. Statistical analyses

Relative merits of using transformed data with ordinary least-squares linear analyses versus using models based on Poisson or negative binomial distribution for analyzing count data have recently been discussed (O’Hara and Kotze, 2010; Ives, 2015; Warton et al., 2016; Morrissey and Ruxton, 2020). The first-mentioned approach provides robust statistical tests for significance and has better type I error rates than the latter approach over a wide range of conditions (Ives, 2015). Therefore, we used \log_{10} -transformed data and general linear mixed models to study if species richness and total abundance in local communities changed from 1951–1970 to 1996–2015 and if the change was dependent on lake type; a significant interaction between “period” and “lake type” would indicate that changes in the community characteristics differ between oligotrophic and eutrophic lakes. Lake and year were included as random factors in both analyses to account for differences between the lakes in species richness and total abundance and in temporal gaps in the data. Tukey’s honestly significant difference test was used as a post-hoc test to verify with pairwise comparisons statistical significance of the lake type-specific changes in species richness and total abundance between the two periods. We used a t -test to test for differences in the community-level SER_a values and the rate of population change of individual species between the lake types and a paired t -test to test for changes in species-specific abundances (\log_{10} -transformed) between the two periods. Effect sizes for the paired t -tests were calculated as the mean difference between the two periods divided by the SD of the mean difference (Lakens, 2013; Dankel and Loenneke, 2018).

3. Results

3.1. Community-level changes

Species richness increased from 1951–1970 to 1996–2015 in the oligotrophic lakes but not in the eutrophic lakes, although the statistically significant main effect “period” indicated an overall increase from 1951–1970 to 1996–2015 (Table 1, Fig. 1a). Total abundance, in turn, showed contrasting patterns between the lake types: increase from 1951 to 1970 to 1996–2015 in the oligotrophic lakes but decrease in the eutrophic lakes, and, hence, no overall difference between the periods (Table 1, Fig. 1b). Species richness and total abundance did not show a temporal trend within any of the period-lake type datasets (Supplementary material, Fig. A4).

SER_a indicated similar levels of change in species proportional abundances between 1951 and 1970 and 1996–2015 for the oligotrophic lakes (mean $SER_a = 0.750$, SD = 0.241, range 0.298–1.0, $n = 15$) and the eutrophic lakes (mean $SER_a = 0.656$, SD = 0.233, range 0.298–1.0, $n = 20$), with no difference in the mean SER_a between the lake types ($t = 1.169$, $df = 33$, $p = 0.251$).

Table 1

Linear mixed model analysis of changes in species richness and total abundance by lake type (oligotrophic or eutrophic) from 1951–1970 (period 1) to 1996–2015 (period 2) in waterbird communities in southern Finland (n = 332 lake-year cases). Lake and year were included as random factors in both analyses. Post-hoc pair-wise comparisons between the periods for each lake type were done with Tukey's honestly significant difference test. See Fig. 1 for model-estimated least squares means of species richness and total abundance by period and lake type.

Species richness	
Effect	
Period	$F_{1,326} = 10.367, p = 0.001$
Lake type	$F_{1,326} = 45.053, p = 0.000$
Period * lake type	$F_{1,326} = 28.009, p = 0.000$
Pair-wise comparisons for period 1 versus period 2 by lake type	
Oligotrophic lakes	$t = -5.332, p = 0.000$
Eutrophic lakes	$t = 1.696, p = 0.326$
Total abundance	
Effect	
Period	$F_{1,326} = 1.849, p = 0.175$
Lake type	$F_{1,326} = 32.618, p = 0.000$
Period * lake type	$F_{1,326} = 28.306, p = 0.000$
Pair-wise comparisons for period 1 versus period 2 by lake type	
Oligotrophic lakes	$t = -4.179, p = 0.000$
Eutrophic lakes	$t = 3.265, p = 0.006$

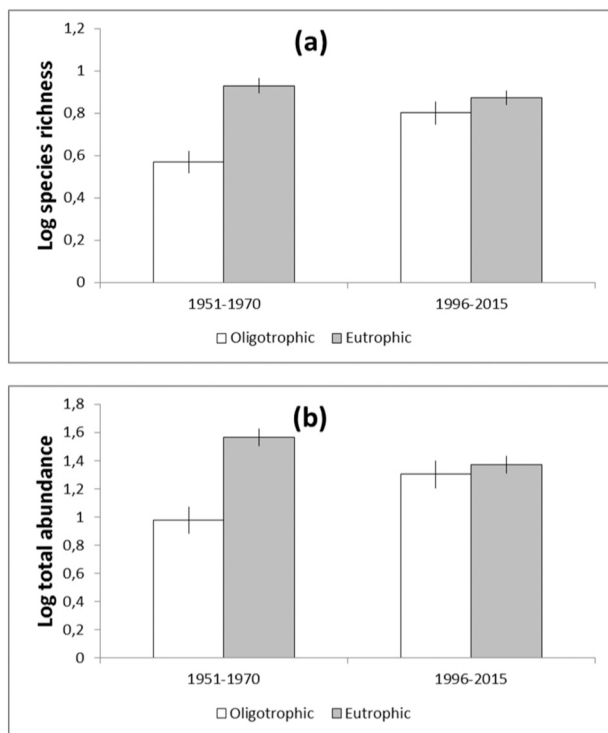


Fig. 1. Least squares means (\pm SE) of (a) species richness and (b) total abundance in 1951–1970 and 1996–2015 for oligotrophic and eutrophic waterbird communities in southern Finland, as estimated by a linear mixed model including the fixed effects “period”, “lake type” and “period * lake type” and random effects “lake” and “year”. See Table 1 and Material and methods for more details.

3.2. Changes in species abundances and proportional abundances

Both increases and decreases in the abundance of individual species from 1951–1970 to 1996–2015 were found in the data pooled from both

lake types: the whooper swan (*Cygnus cygnus*) and common goldeneye (*Bucephala clangula*) increased, whereas the great-crested grebe (*Podiceps cristatus*), horned grebe (*Podiceps auritus*), mallard (*Anas platyrhynchos*), tufted duck (*Aythya fuligula*) and common pochard (*Aythya ferina*) decreased (Table 2).

Comparing changes in abundances between the lake types, population change rate indicated a decline for the Eurasian wigeon (*Mareca penelope*), mallard and common teal (*Anas crecca*) from 1951–1970 to 1996–2015 at the eutrophic lakes but an increase in the Eurasian wigeon and common teal at the oligotrophic lakes; for the mallard, the breeding numbers at the oligotrophic lakes did not change (Fig. 2a; Supplementary material, Table A3). The difference between the lake types was statistically significant in all these species (Eurasian wigeon, $t = 2.166$, $df = 26$, $p = 0.040$; mallard, $t = 2.805$, $df = 29$, $p = 0.009$; common teal, $t = 3.576$, $df = 28$, $p = 0.001$). Population change rate of the whooper swan indicated increase in both lake types (Fig. 2a; Supplementary material, Table A3), although the increase was more pronounced at the eutrophic lakes ($t = 2.844$, $df = 17$, $p = 0.011$). The rate of population increase of the common goldeneye did not differ between the lake types ($t = 0.025$, $df = 29$, $p = 0.981$). Data for the other species were insufficient for testing ($n < 5$ for both lake types).

The changes in species abundances resulted in considerable changes in proportional abundances for both community types (Fig. 2b; Supplementary material, Table A3). Proportional abundance of the common goldeneye (mean proportional abundance, MPA, 0.094 in 1951–1970 and 0.361 in 1996–2015) and Eurasian wigeon (MPA 0.003 in 1951–1970 and 0.119 in 1996–2015) increased in the oligotrophic communities, whereas that of the mallard decreased (MPA 0.418 in 1951–1970 and 0.212 in 1996–2015).

Considering the eutrophic communities, the common goldeneye ranked eighth in abundance in 1951–1970 (MPA 0.060) while it was the most abundant species in 1996–2015 (MPA 0.271). At the same time the tufted duck decreased from the most abundant species in 1951–1970 (MPA 0.161) to the seventh most abundant species in 1996–2015 (MPA 0.051), with corresponding changes occurring for the common pochard and horned grebe (Fig. 2b; Supplementary material, Table A3).

4. Discussion

We found considerable differences in biodiversity change between local waterbird communities that represent the same habitat type (freshwater lakes) and are situated within the same region. Specifically, while species richness at the eutrophic lakes did not change from 1951–1970 to 1996–2015, total waterbird abundance decreased. By contrast, both species richness and total abundance increased from 1951–1970 to 1996–2015 at the oligotrophic lakes. Interestingly, SERa did not reveal differences between the lake types in the level of change in species proportional abundances.

Although species turnover was not specifically studied, it is obvious from the data for the eutrophic lakes that local extinctions were often offset by immigrations, keeping species richness unchanged. For example, local extinction of the horned grebe (the species occurred in a community in 1951–1970 but not in 1996–2015) was offset by whooper swan colonization (the species did not occur in a community in 1951–1970 but did occur in 1996–2015) in eight cases (see Supplementary material, Table A4). However, as revealed by the species-level results, populations of many species declined at the eutrophic lakes to such a degree that the increases of the other species, particularly the whooper swan and common goldeneye, were not sufficient to compensate for the declines. In the oligotrophic lakes, in turn, population increases prevailed and the slight decline of some previously less abundant species, were offset by abundance changes in other species. Our results thus demonstrate that information on local extinction-colonization dynamics is not enough to understand biodiversity change in local communities, nor do measures of turnover by changes in species proportional abundances (e.g. SERa) reveal all important aspects of the

Table 2

Mean and 95% confidence limits of population change rate ($(\log_{10}(\text{mean abundance in 1996–2015} + 1)) - (\log_{10}(\text{mean abundance in 1951–1970} + 1))$) of 18 species in waterbird communities in southern Finland. A *t*-test was done for species with sample size $n \geq 5$ (number of communities). Effect sizes (converted to positive values) were calculated as the mean difference between the two periods divided by the SD of the mean difference. Species abbreviations are given in parentheses after the scientific name (cf. Fig. 2). Species are grouped according habitat preference (Lehikoinen et al., 2016).

Species	Mean	95% LL	95% UL	n	t	p	Effect size
Species preferring oligotrophic lakes							
Black-throated diver, <i>Gavia arctica</i> (Garc)	0.112	-0.095	0.320	7	1.323	0.234	0.500
Red-throated diver, <i>Gavia stellata</i> (Gste)	-0.167	-0.338	0.004	5	2.717	0.053	1.210
Goosander, <i>Mergus merganser</i> (Mmer)	0.225	-0.054	0.505	4			
Species preferring eutrophic lakes							
Great crested grebe, <i>Podiceps cristatus</i> (Pcri)	-0.177	-0.299	-0.056	11	3.262	0.009	0.983
Red-necked grebe, <i>Podiceps grisegena</i> (Pgri)	0.035	-0.149	0.220	12	0.422	0.681	0.121
Horned grebe, <i>Podiceps auritus</i> (Paur)	-0.355	-0.527	-0.184	17	4.393	0.000	1.066
Northern pintail, <i>Anas acuta</i> (Aacu)	-0.058	-0.607	0.491	3			
Garganey, <i>Spatula querquedula</i> (Sque)	-0.046	-0.186	0.093	8	0.783	0.459	0.275
Shoveler, <i>Spatula clypeata</i> (Scly)	-0.139	-0.272	-0.006	10	2.364	0.042	0.747
Common pochard, <i>Aythya ferina</i> (Afer)	-0.295	-0.532	-0.058	17	-2.643	0.018	0.641
Common coot, <i>Fulica atra</i> (Fatr)	-0.141	-0.339	0.057	14	-1.541	0.147	0.410
Species occurring frequently in both lake types							
Whooper swan, <i>Cygnus cygnus</i> (Ccyg)	0.216	0.159	0.273	19	8.001	0.000	1.831
Canada goose, <i>Branta canadensis</i> (Bcan)	0.059			1			
Eurasian wigeon, <i>Mareca penelope</i> (Mpen)	0.060	-0.078	0.198	28	0.892	0.380	0.169
Mallard, <i>Anas platyrhynchos</i> (Apla)	-0.164	-0.264	-0.063	31	3.337	0.002	0.601
Common teal, <i>Anas crecca</i> (Acre)	-0.123	-0.254	0.008	30	1.924	0.064	0.350
Common goldeneye, <i>Bucephala clangula</i> (Bcla)	0.345	0.229	0.462	31	6.054	0.000	1.088
Tufted duck, <i>Aythya fuligula</i> (Aful)	-0.370	-0.581	-0.160	17	-3.730	0.002	0.902

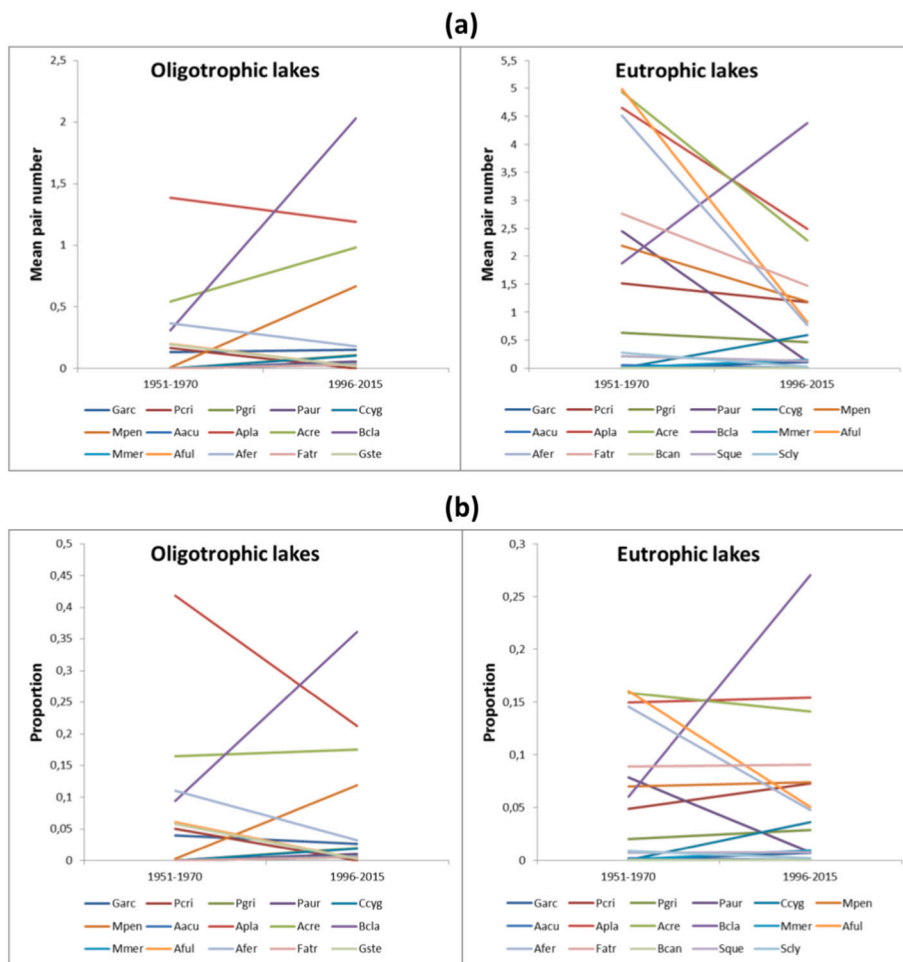


Fig. 2. Changes in (a) species-specific abundances and (b) species proportional abundances from 1951–1970 to 1996–2015 in oligotrophic (left panel) and eutrophic (right panel) waterbird communities in southern Finland. See Table 2 for species abbreviations. The end points of the species-specific lines give the overall means for the lake types and periods, calculated using all lake-year cases (surveys) and including zeroes for each species (see Supplementary material, Table A3 for numerical values). Note that the scale of the y-axis differs between the oligotrophic and eutrophic lakes for both metrics.

change. Clearly, we need to examine in detail what happens with the abundances of individual species to understand changes at the community level (Schipper et al., 2016; Dornelas et al., 2019).

The case of the whooper swan exemplifies the different roles that changes in abundance versus occupancy may have in affecting biodiversity change in local communities. The whooper swan contributed importantly to the species richness of the relatively species-poor local communities studied here. However, even though the whooper swan was widespread in 1996–2015, its local abundance was consistently low and, hence, its contribution to the total abundance negligible, particularly in the eutrophic communities. This finding underscores the concern that, although changes in local species richness may not occur due to species turnover (e.g. Dornelas et al., 2014), immigrating species may have different ecological functions than species that have become extinct (Supp and Ernest, 2014; Jarzyna and Jetz, 2017), the functional differences stemming particularly from differences between the species in local abundance (Inger et al., 2015; Schipper et al., 2016). For example, the whooper swan and horned grebe clearly cannot be considered ecological counterparts. The whooper swan is a large herbivore, with low local abundance everywhere (see also Pöysä et al., 2018), whereas the horned grebe is a small invertivore, often reaching high numbers in local communities (this study: annual maximum 22 pairs per community in 1951–1970).

All in all, the differences between the lake types in terms of changes in species richness and abundances are surprising, considering that the study lakes are situated within the same region and, hence, have a common species pool and are affected by the same global drivers. The breeding numbers of three species decreased in the eutrophic lakes but increased or remained stable in the oligotrophic lakes, while the breeding numbers of four other species that prefer eutrophic lakes showed an overall decline (Table 2). This corroborates the findings of Lehikoinen et al. (2016) and suggests that the population declines might be connected with eutrophication per se, probably via impacts on food supply and nest site availability. However, several lines of evidence suggest that excessive eutrophication may not be the sole driver of the changes in eutrophic lakes. First, the common goldeneye belongs to the same foraging guild and has the same diet type as the common pochard and tufted duck (Pöysä, 1983; Elmberg et al., 2020). The decline of the two latter species in eutrophic lakes during the last three decades has been attributed to presumed deterioration of foraging conditions due to excessive eutrophication (e.g. Fox et al., 2016, 2019; Lehikoinen et al., 2016). The increase of the common goldeneye in the eutrophic lakes, however, conflicts with this idea, because deterioration of foraging conditions in eutrophic lakes should have affected this species negatively, too. On the other hand, given that some species have increased while others have decreased, one might suggest that interspecific competition for food has played a role in affecting the changes in the waterbird communities. However, the observation that species' abundances are inversely correlated may not indicate competition but contrasting species-specific responses to changing environmental conditions (Pöysä, 1984; Nudds, 1992). For example, the contrasting population trends of whooper swan and horned grebe clearly cannot be attributed to interspecific competition (see above). Second, the species that have declined particularly in eutrophic lakes, such as the great-crested grebe, horned grebe, Eurasian wigeon, common pochard, tufted duck and common coot (*Fulica atra*; Lehikoinen et al., 2016; this study), belong to several foraging guilds and have different diet types (Pöysä, 1983; Elmberg et al., 2020). Therefore, it is difficult to attribute the declines of all these species to a single, foraging conditions-related driver. Similarly, negative impacts of eutrophication on nest site availability seem unlikely as a general driver of waterbird declines at eutrophic lakes, because species with very different nest sites have declined there. For example, great-crested grebe, horned grebe and common pochard typically nest in water or close to water in cover of emergent vegetation, whereas Eurasian wigeon, mallard and common teal nest far from water, typically in shore forests (Väänänen et al.,

2016).

Increased nest predation may have played an important role in the population declines of many species from 1951–1970 to 1996–2015, probably more at the eutrophic lakes than at the oligotrophic lakes (see also Holopainen et al., 2020a). Eutrophic lakes typically are surrounded by agricultural areas, and nest depredation experiments suggest that agricultural landscapes maintain higher levels of predation pressure on duck nests than do forested areas (Gunnarsson and Elmberg, 2008; Holopainen et al., 2020b). The American mink and raccoon dog have increased strongly in the study area and elsewhere in southern Finland since the 1951–1970 period (Helle and Kauhala, 1991; Kauhala, 1996a). Most likely, predation pressure by these alien species has remained high over the last decades as suggested by the development of the hunting bag of the species in Finland from 1951–1970 to 1996–2015. The annual hunting bag of American mink in Finland increased from less than 1000 individuals in the early-1960s to about 70,000 in the mid-1980s (Kauhala, 1996a, 1996b), the corresponding increase being from zero to about 60,000 for raccoon dog (Helle and Kauhala, 1991; Kauhala, 1996c). After the increase phase, the hunting bag has remained high for both species, including the period 1996–2015 (Supplementary material, Fig. A5). Hence, their role in waterbird population declines cannot be excluded, although other nest predators, such as corvids, may also have contributed to the declines, particularly after the collapse of protective gull colonies (Pöysä et al., 2019c). A recent study from Poland demonstrated that the population declines of many waterbird species in different parts of the country coincided with the regional increase of the American mink, although delays in the response to the American mink invasion occurred (Brzeziński et al., 2020). The common goldeneye versus common pochard–tufted duck paradox (see above) is also congruent with the alien predator hypothesis and the increased nest predation hypothesis in general. The two latter species are “ground-nesters”, typically placing the nest in the littoral zone near edges of emergent vegetation; therefore, they are highly vulnerable to many nest predators, including the American mink and raccoon dog (Nummi et al., 2019; Pöysä et al., 2019c). Common goldeneye, in turn, is a cavity-nesting species, largely avoiding nest predators, other than the pine marten (*Martes martes*; Pöysä et al., 1997). Common pochard and tufted duck obviously benefit from the presence of gull colonies (Väänänen, 2001; Pöysä et al., 2019c), whereas common goldeneye does not show association with gulls (Pöysä et al., 2019c).

The abundance change of many species from 1951–1970 to 1996–2015 (this study) is congruent with the population growth rate of the same species during the period 1986–2013 (Lehikoinen et al., 2016). For example, the great-crested grebe, horned grebe, tufted duck and common pochard showed a decline in both datasets. However, contrasting patterns can also be recognized, three of which are worth mentioning. The mallard declined drastically from 1951–1970 to 1996–2015, whereas its population growth rate indicated an increase during 1986–2013. The common goldeneye, in turn, increased considerably from 1951–1970 to 1996–2015 but showed no trend in 1986–2013. Finally, the Eurasian wigeon showed no overall change from 1951–1970 to 1996–2015 but it declined during 1986–2013.

The patterns of population changes, as found in this study and in Lehikoinen et al. (2016), demonstrate that boreal waterbird communities change continuously (see also Pöysä et al., 2019a; Elmberg et al., 2020). It is important to note in this context that populations of many species that prefer eutrophic lakes, such as the common pochard and common coot, increased in Finland and other north European countries in 1850–1970 (Järvinen and Ulfstrand, 1980). Interestingly, these historical population increases and immigrations have been attributed to human-caused eutrophication (von Haartman, 1973; Järvinen and Ulfstrand, 1980). Specifically, eutrophication of previously nutrient-poor boreal lakes has created opportunities (more food and sheltered breeding habitat) for migrating species to colonize the lakes. It is not known when the species that are currently declining in eutrophic lakes reached their highest numbers. Nevertheless, if eutrophication has been

the main driver of their breeding numbers since the 1850s, as previous authors have asserted, its effect has turned from positive to negative, probably at some point between 1951–1970 and 1996–2015. This finding further underlines the importance of properly defining the temporal baseline against which population and biodiversity changes are evaluated, to set biologically realistic goals for conservation and management decisions and measures (cf. Collins et al., 2020).

Data on temporal trends in water chemistry variables indicating eutrophication (e.g. total phosphorous, or TP, total nitrogen, or TN; and chlorophyll α ; Ekholm and Mitikka, 2006) are not available from our study lakes. In general, a recent analysis suggests that TP and TN loads originating from diffuse sources, especially those from agriculture, have not decreased in Finland during the recent decades (Räike et al., 2020). Moreover, recovery from eutrophication caused by agricultural over-enrichment of soils has been predicted to take potentially hundreds of years (Carpenter, 2005). As the eutrophic lakes in our study area are located at lower elevations and typically are surrounded by agricultural areas (i.e., are more vulnerable to anthropogenic eutrophication; see Section 2.1 Study lakes), it is likely that significant recovery from eutrophication has not occurred in the lakes from 1951–1970 to 1996–2015. In line with this interpretation, while clear changes in species composition (mainly gain of new species) of aquatic plant communities in lakes in the nearby study area has occurred from the 1940s to the 1970s, temporal changes in the aquatic plant communities have been modest from the 1970s to the 2010s (Lindholm et al., 2021).

We have focused on eutrophication and predation as main drivers of changes in waterbird populations and communities from 1951–1970 to 1996–2015. Possible alternative drivers could be changes in hunting pressure (Pöysä et al., 2013), human disturbance (Carney and Sydesman, 1999), fish competition (Nummi et al., 2016) and protection status of the lakes (Pavón-Jordán et al., 2020), as well as divergent impacts of changes in wintering conditions depending on wintering area (Pavón-Jordán et al., 2018). We do not have data on changes in local hunting pressure, human disturbance or fish abundances to assess if changes in them could explain long-term changes in waterbird populations and communities in the study lakes, particularly the divergent trends between oligotrophic and eutrophic lakes. In general, a comparison of long-term population trends between protected and huntable species suggested that hunting per se is not an important driver of population changes in boreal waterbird communities, except mallard (Pöysä et al., 2013). Mallard is the most important game species in Finland and other north European countries (Dalby et al., 2013a). It is possible that hunting pressure was too high in the years between the study periods 1951–1970 and 1996–2015, and this is reflected in the population decline of the mallard from the 1951–1970 level. For example, the ban of led shot in Finland in 1996 resulted in an abrupt reduction of about 29% in total mallard harvest, and breeding numbers of mallard started to increase after that, while they did not show a trend in 1986–1996 (Pöysä et al., 2013). This finding, of course, does not explain why breeding numbers of mallard declined from 1951–1970 to 1996–2015, but it supports the idea that breeding numbers of the species may respond to changes in hunting pressure (see also Reynolds and Sauer, 1991). It is possible that human activity at the study lakes has increased from 1951–1970 to 1996–2015, with possible harmful effects on some species. From the species studied here, the red-throated diver (*Gavia stellata*) has been considered particularly sensitive to human disturbance (Nummi et al., 2013). However, because red-throated diver does not breed at eutrophic lakes (Supplementary material, Table A4), possible harmful effects of human disturbance on its numbers cannot explain the changes in waterbird communities documented here; total waterbird abundance decreased from 1951–1970 to 1996–2015 in eutrophic lakes but increased in oligotrophic lakes. Impacts of fish on waterbirds often are associated with changes in the composition of fish communities due to excessive eutrophication resulting in the increase of cyprinid species (Rask et al., 2010). Hence, impacts of fish on waterbirds usually are considered under the general impacts of eutrophication (discussed

above). An analysis of species traits, such as main wintering areas, is out of the scope of this study. Results of this study and earlier studies together suggest that wintering area per se may not be important in affecting long-term population changes of waterbirds. For example, mallard and common teal, both species being dependent on shallow water and thus particularly vulnerable to changes in wintering conditions, had similar population trends (Table 2) despite having markedly different wintering areas and strategies in Europe (Dalby et al., 2013a, 2013b; Arzel et al., 2014). When it comes to protected areas, four of the eutrophic lakes (IDs 1, 2, 3 and 7 in Supplementary material, Table A1) of this study are in the Natura 2000 protected areas network of the EU. This has not, however, helped to maintain favorable status of waterbird biodiversity in these lakes, because populations there have declined considerably from 1951–1970 to 1996–2015 (H. Pöysä and P. Linkola, unpublished). Finally, the increase of the common goldeneye from 1951–1970 to 1996–2015 probably is due to nest box provisioning programs that started in Finland in the 1950s (Sirén, 1951; see also Pöysä and Pöysä, 2002). Long-term changes in the abundance of pine marten, the main nest predator of common goldeneye (see above), in Finland are not well known, but hunting bag statistics suggest that, if anything, their population has increased from the 1960s to the 1990s (Helle, 1996). This suggests that the long-term increase of the common goldeneye cannot be attributed to decreased predation risk.

5. Conclusions and conservation implications

Our study has several general conservation implications. First, decision makers and conservation practitioners should consider that current monitoring programs may not be suitable to set biologically reasonable temporal baselines for assessing changes in species abundances and biodiversity in local communities (cf. Mihoub et al., 2017). A longer and biologically more relevant time scale to assess the impact of a particular driver may reveal that the status of a given biodiversity component is worse (or better) than the current monitoring data suggest. Second, as also underlined by Dornelas et al. (2019), whole-assemblage monitoring data are of vital importance for biodiversity conservation, as they enable a more comprehensive understanding of biodiversity change in local communities, and ultimately globally. Efforts to improve whole-community monitoring should be increased.

The last point above translates to practical conservation implications concerning waterbird communities. Ecological conditions in boreal lakes have deteriorated due to multiple stressors. Hence, local abundances of different species likely are affected by different drivers, calling for an autecological or nesting guild-specific emphasis in the conservation management of these systems. For example, overgrowing of open water areas due to extending floating-leaved vegetation (often associated with hyper-eutrophication) obviously is more deleterious to diving than surface-feeding species. Hence, vegetation removal (e.g. Lehtikoinen et al., 2017) is needed to aid diving species particularly to recover, a management measure that simultaneously improves ecological conditions for other taxa, such as light-dependent bottom fauna and flora. As another example, species nesting among emergent vegetation in the littoral zone and near the shoreline are more vulnerable to invasive predators than species nesting in tree cavities or on the ground further away from the shore line (Pöysä et al., 2019c; Brzeziński et al., 2020). Hence, control of alien predators is also needed but, again, the effect of such a measure probably is species-specific (Nummi et al., 2019; Brzeziński et al., 2020).

Finally, our data are from one boreal region only, and it would be informative to get historical data from other boreal regions to confirm the generality of the findings of this study. Notwithstanding, because the birds breeding in Finland constitute a considerable proportion of the European breeding population for many waterbird species (see Hage-meijer and Blair, 1997), we believe that the results of this study are important to the conservation of European waterbird populations and communities and biodiversity in boreal lakes in general.

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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Dedicated to the memory of Pentti Linkola, an uncompromising and exemplary conservationist.

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Appendix A. Supplementary data

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