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Variation in population trends and spatial dynamics of waterbirds in a boreal lake complex

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Breeding waterbird populations were studied in a boreal lake system between 1986 and 2012 to find out whether there are differences in temporal trends and spatial variation between waterfowl, grebe, diver and gull species. The study was based on censusing all waterbirds in a lake complex of 45.75 km^2 of water area and 290 km of shoreline length (scale 1:20,000), and the results were compared with the changes in water quality during the study period. The population density of species varied significantly between the water bodies, showing that waterbird species prefer certain water bodies within the lake system. Spatial variation of many waterfowl – gull species and diver – gull species pairs were similar probably due to heterospecific attraction or similarities in habitat preferences. The temporal density change of breeding ducks and grebes was high: seven of the eight most abundant species showed significant temporal density patterns, having either linear (negative) trend or non-linear (quadratic, first increase then decrease) population change. Pooled pair numbers of waterfowl species were first stable, but declined drastically by half between 2003/2004–2012. In contrast, two out of four gull species increased, and the Black-throated Diver did not show any significant trend. Water clarity in the lake complex had decreased during the study period, which may have been one reason causing the population changes of waterbirds, because the increase in turbidity largely explained the negative trend of declining ducks. Climate change may accelerate eutrophication, having, in turn a negative effect on waterbird populations.

1. Introduction

Populations of species vary in both time and in space at different scales. The temporal dynamics of bird species are generally well known compared to many other taxa (see e.g., Perrins *et al.* 1991), and the knowledge and prediction of the spatiotemporal variation of bird species is vital for understanding population dynamics and for the conservation of species (Virkkala 1995). In general, the dynamics of bird species are affected by habitat changes, climatic variation, species-specific life-history characteristics, variations in food resources, and species interactions (e.g., Perrins *et al.* 1991, Virkkala 1995, Sæther *et al.* 2005, Møller *et al.* 2010). Temporal variations also typically increase towards species range margins, so that marginal populations suffer greater fluctuations in abundance than do central populations (Williams *et al.* 2003, Cuervo & Møller 2013). Temporal population change consist both of short-term year-to-year fluctuation and long-term population trends.

Climate change increasingly affects range shifts of species (Chen *et al.* 2011, Bellard *et al.*

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2012). Due to climate change, the ranges of bird species are predicted to shift polewards and towards mountain tops (Huntley *et al.* 2007, Barbet-Massin *et al.* 2012, Virkkala *et al.* 2013). The population dynamics of bird species in Europe has been linked to the predicted range shifts: species predicted to gain range have increased and those predicted to lose range have decreased (Gregory *et al.* 2009). In addition, species that have declined did not advance their spring migration, whereas those with stable or increasing populations advanced their migration considerably (Møller *et al.* 2008). Thus, population trends in birds were related to the effects of climate change.

Virkkala (2006) showed that the spatiotemporal dynamics of gull species (*Larus* spp) in a boreal lake complex in Finland varied between species. The most abundant gull species, the Common Gull (*Larus canus*), had a low spatial turnover in nesting sites during the study period. In contrast, the Red-Listed gull species had a much higher spatial turnover, for which reason they would easily disappear from a single site. Populations of breeding waterbirds (ducks, grebes and divers) have recently shown considerable population declines in Finland, presumably due to habitat alteration caused by increased eutrophication (Pöysä *et al.* 2013). Eutrophication of lakes is partly a consequence of climate change with mild and rainy winters increasing the runoff of nutrients from the fields in the catchment area (Puustinen *et al.* 2007). An important question is whether there are patterns in the temporal trends of waterbirds that would make them susceptible to increased effects of climate change, which are manifested, for instance, in increased eutrophication levels. Temporal trends are regarded here as linear trends (negative or positive) or as non-linear with variation between years.

In this work, the temporal population change of breeding waterfowl (ducks, geese and swans), divers, grebes and gulls was studied in a boreal lake complex from 1986 to 2012. In contrast to other waterbirds, gulls more commonly use terrestrial habitats in their foraging (particularly fields and dumps). The purpose of the study is to compare temporal change and spatial dynamics of waterfowl, diver and grebe species with those of gull species. This is vital for planning conservation measures for species at a proper scale, as negative or positive population trends can be reflections of environmental changes. The main questions addressed in this study were: (1) Are the population trends, linear and non-linear, different between the different waterbird species? (2) Do the population densities of species differ spatially? (3) What are the consequences temporal population changes and spatial dynamics of boreal waterbirds for conservation planning?

2. Material and methods

2.1. Study area

The Kukkia lake complex is situated in southern boreal Finland (61°20’ N, 24°45’ E, see Fig. 1). The catchment area of Kukkia consists of approximately 85% of forested areas and 15% of agricultural and built-up areas. Kukkia consists of different, isolated water bodies connected with narrow straits. The characteristics of the water bodies of Kukkia lake complex are presented in Supporting Information Table S1. The total water area and shoreline length were measured from an electronic version of a map at 1:20,000 by ArcView. The total water area is 45.75 km^2 and the shoreline length is 290 km. The mean depth of water areas is 5.7 m, and the deepest point is 34 m (Mäkirinta 1978). The Kukkia lake complex is characterized by forested islands and islets (Fig. 1), where many waterbird species breed. There are a total of 52 islands larger than 1 ha, and 11 larger than 10 ha, the two largest islands exceeding 60 ha. Along the shorelines and also even in the middle of water bodies there are many rock outcrops and boulders, on which gulls typically breed. Kukkia is an unregulated lake system belonging to the Hauho watercourse of oligo-mesotrophic lakes.

In its nutrient status, the lake complex is mainly oligotrophic with some mesotrophic and eutrophic areas (Mäkirinta 1978). The most eutrophicated water area is Rautajärvi (see Fig. 1), where there are also the largest stands of the Common Reed (*Phragmites australis*). No major changes occurred in the patterns of shoreline vegetation during the study period. Water quality variables are sampled and measured each year at the same site (see Fig. 1) in August–September by the Environmental Authorities (data gathered in the Finn-

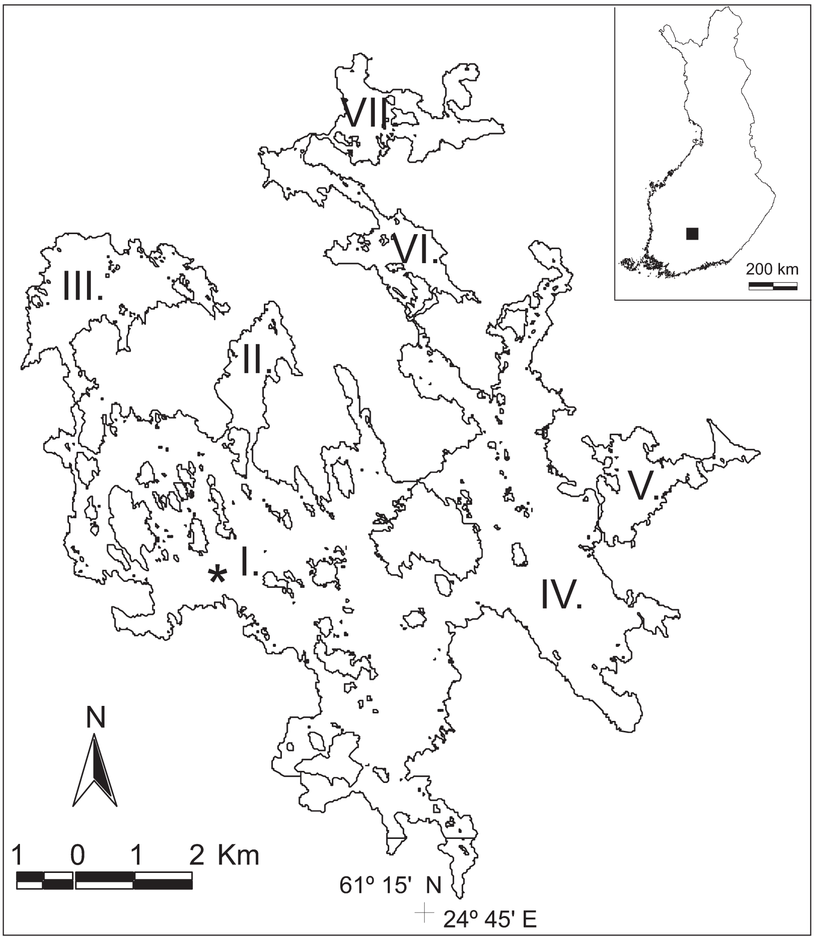

Fig. 1. Situation of the Kukkia lake complex in southern Finland. The different water bodies: I. = Western main Kukkia, II. = Rihanselkä, III. = Haltianselkä, IV. = Eastern main Kukkia, V. = Leppänä, VI. = Läyliä & Äikkäänselkä, VII. = Rautajärvi. Asterisk denotes the site, where water quality variables were sampled annually in western main Kukkia in 1986–2012. (National Land Survey of Finland, Permit number MML/VIR/TIPA/182/10)

ish Environment Institute, for the variables and their measurement; see Mitikka & Ekholm 2003). In Fig. 2, the values of total phosphorus (Total P, µg / l), total nitrogen (Total N, µg / l), chlorophyll *a* (µg / l) turbidity (FNU, Formazin Nephelometric Unit) and Secchi depth (m) are presented, based on annual samples (at a water depth of 1 m) in 1986–2012. Values of Total P, Total N and chlorophyll *a* have not changed during the study period, so there are no clear signs of eutrophication. However, the value of turbidity has increased and that of Secchi depth has decreased (both particularly after 2004) showing a slight decline in overall water quality. In addition, summer residences have been built (particularly from the 1960s to the 1980s) along the shores and islands. At present, there are about 1,000 summer residences along the shores of Kukkia.

The main water bodies of Kukkia (western and eastern main Kukkia, Haltianselkä, Rihanselkä, see Fig. 1) belong to the Natura 2000 network based on the Habitats Directive (Ministry of the Environment 1999). The Kukkia lake complex (all water bodies except Rautajärvi) belongs to the network of Important Bird Areas in Europe (IBA) mainly due to its large populations of Common Gull, Lesser Black-backed Gull (*Larus fuscus*) and Black-throated Diver (*Gavia arctica*) (Heath & Evans 2000; see Supporting Information Table S2).

Change in climate variables during the study period was investigated by studying changes in mean annual temperature and in mean temperature of April–June in the four 10 × 10 grid cells where the Kukkia lake complex is situated. These data of climate variables are based on 10 × 10 km gridded data obtained from the Finnish Meteorological Institute (Tietäväinen *et al.* 2010). Mean annual tem-

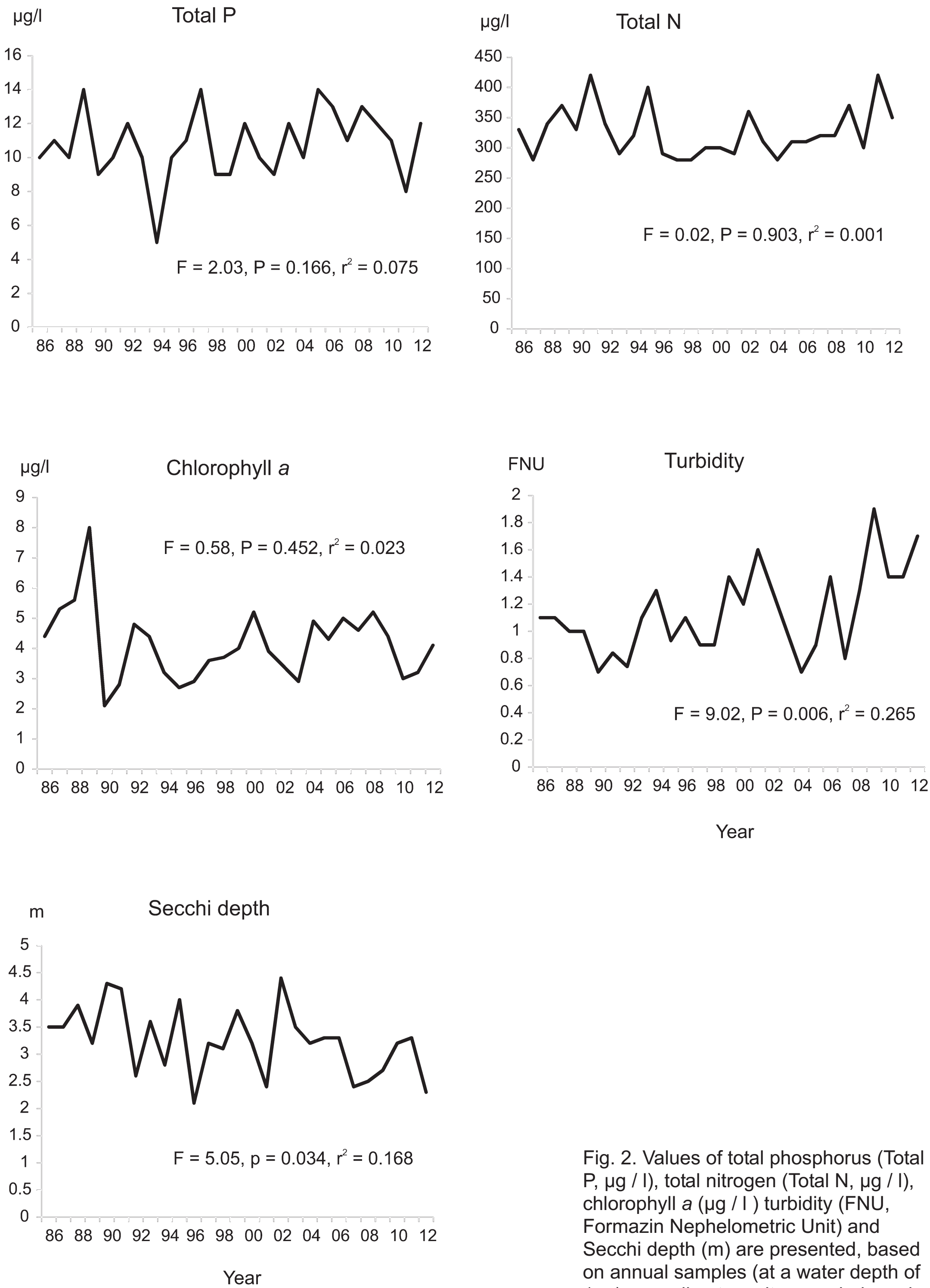

Fig. 2. Values of total phosphorus (Total P, µg / l), total nitrogen (Total N, µg / l), chlorophyll *a* (µg / l) turbidity (FNU, Formazin Nephelometric Unit) and Secchi depth (m) are presented, based on annual samples (at a water depth of 1 m) according to a site sampled yearly in 1986–2012 in August–September (data in Finnish Environment Institute).

perature has risen by about 1.2°C ($y = 0.046x + 3.742$) and mean April–June temperature by about 0.5°C ($y = 0.018x + 8.756$) in the study area during the study period (1986–2012).

2.2. Bird censuses

Breeding waterbirds were counted by the author in each study year between 13 and 22 May in exactly the same way, by rowing a boat around all the shorelines, rocks and rock outcrops. The bird censuses were related each year to ice-breaking, so that the censuses were carried out exactly 12–20 days after ice-breaking, which occurred on average on 2nd May (range 27th April–7th May) during the study years. All the areas were later checked each year in late June–early July to discover the possible late breeders. Birds were counted in four census periods: in 1986/87, in 1998/99, in 2003/04, and in 2012. The western parts of Kukkia (western main Kukkia, Rihanselkä, Haltianselkä) were counted in the first study year in every census period (1986, 1998, 2003) and the eastern and northern parts (eastern main Kukkia, Leppänä, Läyliä & Äikkäänselkä, Rautajärvi) in the second study year (1987, 1999, 2004). In 2012 the whole lake complex was counted in the same year. All the censuses were carried out by the author.

Among the waterfowl, divers and grebes as a breeding pair was interpreted as an observed pair, a male or a female (see Koskimies & Väisänen 1991). In the Whooper Swan (*Cygnys cygnus)* and in the Black-throated Diver only clearly observed pairs were recorded as breeding pairs in contrast with non-breeding single individuals or flocks. Gulls were mostly incubating or in some cases building a nest.

Pairs of each species were mapped based on the counts and pair numbers were summed in each water body. Densities were calculated based on the number of pairs per kilometre of shoreline in each of the water body. Shoreline was measured at the scale of 1:20,000 (see Table S1). Mean density (± SE) of each species in the whole lake complex in each year(s) was calculated as mean of the densities in the different water bodies ($N = 7$).

Altogether, 16 species of waterfowl, divers and grebes and four species of gulls were observed (see Table S2). Of the waterfowl, divers and grebes, the nine most abundant species with a total sample size of over 100 pairs (mean number of pairs over 25 in each census period) were included in the species-specific analyses: Eurasian Wigeon (*Anas penelope*), Common Teal (*A. crecca*), Mallard (*A. platyrhynchos*), Common Pochard (*Aythya ferina*), Common Goldeneye (*Bucephala clangula*), Red-breasted Merganser (*Mergus serrator*), Common Merganser (*M. merganser*), Black-throated Diver, and Red-necked Grebe (*Podiceps grisegena*). All the four gull species were included in species-specific analyses.

Of the nine most abundant waterfowl, diver and grebe species studied, seven could be regarded as species of conservation concern, belonging to at least one of the species classifications (Supporting Information Table S3). Three of the four gull species belong to at least one of the classifications dealing with species conservation concern (Table S3). For example, Common Pochard, Red-breasted Merganser and Lesser Black-backed Gull are regarded as endangered, Eurasian Wigeon, Common Merganser and Black-headed Gull (*Chroicocephalus ridibundus*) as vulnerable according to the Red-Listing of Finnish species (Tiainen *et al.* 2016). Eurasian Wigeon, Common Teal, Common Goldeneye, Red-breasted Merganser, Common Merganser and Lesser Black-backed gull are species of special responsibility in Finland; more than 15% of European populations breed in Finland (Rassi *et al.* 2001). Common Pochard, Black-throated Diver and Common Gull are species of European conservation concern (SPEC2 or SPEC3; BirdLife International 2004). In addition, the Black-throated Diver is regarded as an EU BIRDS Directive species (Annex I). Breeding Lesser Black-backed Gulls belong to the nominate subspecies *Larus f. fuscus*, which only breeds in Fennoscandia (NW Europe; Hagemeijer & Blair 1997, Väisänen *et al.* 1998).

Of the less abundant waterbird species, the Tufted Duck (*Aythya fuligula*) is a species of European concern (SPEC3; BirdLife International (2004)), a species of special responsibility in Finland (Rassi *et al.* 2001) and a Red-Listed species (endangered) in Finland, Great Crested Grebe (*Podiceps cristatus*) a Red-Listed species (near-threatened) and the Whooper Swan is regarded as EU BIRDS Directive species (Annex I). Thus, the waterbird communities in the Kukkia lake com-

Table 1. The significance of spatial density variation and temporal density change in waterfowl, divers and grebes, and in gulls based on general linear model with site as a factor variable and years as covariates (linear and quadratic; df = 1, 6).

Species group	Factor		Covariates			
			Linear		Quadratic	
	F	*P*	*F*	*P*	*F*	*P*
Waterfowl, divers and grebes	42.766	< 0.001	31.433	0.001	10.781	0.017
Gulls	26.278	0.002	0.240	0.641	0.249	0.636

Table 2. The significance of spatial density variation and temporal density change in the most abundant waterfowl, diver and grebe species (A.) and in all the gull species (B.) based on general linear model with site as a factor variable and years as covariates (linear and quadratic; df = 1, 6).

	Factor		Covariates			
			Linear		Quadratic	
Species	*F*	*P*	*F*	*P*	*F*	*P*
A.						
Eurasian Wigeon (*Anas penelope*)	63.032	< 0.001	10.110	0.019	8.470	0.027
Common Teal (*A. crecca*)	91.758	< 0.001	7.613	0.033	0.041	0.846
Mallard (*A. platyrhynchos*)	140.007	< 0.001	0.385	0.558	0.001	0.981
Common Pochard (*Aythya ferina*)	8.474	0.027	8.147	0.029	0.006	0.940
Common Goldeneye (*Bucephala clangula*)	73.309	< 0.001	7.908	0.031	28.274	0.002
Red-breasted Merganser (*Mergus serrator*)	13.602	0.010	6.545	0.043	0.502	0.505
Common Merganser (*M. merganser*)	21.053	0.004	7.028	0.038	3.601	0.107
Black-throated Diver (*Gavia arctica*)	88.535	< 0.001	0.197	0.673	0.000	0.998
Red-necked Grebe (*Podiceps grisegena*)	15.630	0.008	1.802	0.228	17.288	0.006
B.						
Black-headed Gull (*Chroicocephalus ridibundus*)	5.999	0.050	0.046	0.837	0.738	0.423
Common Gull (*Larus canus*)	67.660	< 0.001	7.917	0.031	7.523	0.034
Lesser Black-backed Gull (*L. fuscus*)	8.897	0.025	0.826	0.398	4.153	0.088
Herring Gull (*L. argentatus*)	5.602	0.056	11.722	0.014	0.303	0.602

plex are of high priority in terms of European bird conservation.

Based on habitat selection patterns, three of the most abundant waterfowl, diver and grebe species were regarded as preferring eutrophic lakes, three as preferring oligotrophic lakes and three as generalist according to Pöysä *et al.* (2013) (Table S3); for the classification of species, see also Kauppinen (1993). In addition to the most abundant species, spatiotemporal patterns of less abundant declined species are presented. Pair numbers of all waterbird species in the total lake complex are presented in the Table S2.

2.3. Statistical analyses

A general linear model was used to study the significance of temporal change in bird abundance with site as a factor variable and time as a covariate. Between-subject effect in the analyses shows the difference in the abundance of species between the different water bodies. Time (year) here represents a quantitative, repeated factor, the effects of which can be examined using polynomial contrasts (Gurevitch & Chester 1986, Quinn & Keough 2002). A significant first degree (linear) polynomial indicates a significant linear relationship between bird abundance and year (increase or decrease in abundance over time). A significant second degree (quadratic) polynomial contrast shows a significant non-linear (curvilinear) relationship in bird abundance (see Blake *et al.* 1994). Original density values were log(x + 1) transformed for all the analyses.

3. Results

The density of both waterfowl, divers and grebes, and gulls varied spatially between the different water bodies, because the factor (sites) was significant for both species groups in the general linear models (Table 1). However, both linear trend and non-linear temporal change was significant only in the waterfowl, divers and grebes, in which the linear trend was negative, and thus these species had declined during the study period. Mean density (± SE) of waterfowl, divers and grebes was 2.14 ± 0.29 pairs / km of shore line and that of gulls 3.57 ± 0.35 pairs / km.

In a species-specific comparison, all species, except for the Herring Gull (*Larus argentatus*), showed significant spatial variation ($P < 0.05$) in the analysis, i.e. their densities varied between the different water bodies (Table 2).

Temporal dynamics showed contrasting patterns in the species-specific analyses: seven of the nine waterfowl, diver and grebe species had significant temporal change, either negative linear trends or quadratic variation pattern, whereas two gull species, the Common Gull and the Herring Gull, both increased significantly (Table 2 and Fig. 3). Six waterfowl species (Eurasian Wigeon, Common Teal, Common Pochard, Common Goldeneye, Red-breasted Merganser and Common Merganser) showed a significant, negative linear trend and the three waterfowl and grebe species with significant quadratic variation first increased and then decreased (Eurasian Wigeon, Common Goldeneye, Red-necked Grebe; Fig. 3). For example, Common Goldeneye was clearly the most abundant waterfowl species in 1986–2004, but its densities had collapsed by over 70% by 2012 (Fig. 3 and Table S2). In the Eurasian Wigeon and Common Goldeneye both linear trend and quadratic dynamics were significant (Table 2 and Fig. 3). The pooled pair numbers of waterfowl species remained the same between 1986/87, 1998/99 and 2003/04 with total pair numbers in the lake complex being 524, 517 and 527, respectively, but declined quite drastically by almost half (by 48.4%) between 2003/2004 and 2012 (272 pairs, see Table S2).

Spatiotemporal dynamics is illustrated in the Red-Listed Great Crested Grebe, a less abundant species, the populations of which collapsed during the study period, from 27 breeding pairs in the total lake complex in 1986/87 to four pairs in 2012 (see Fig. 4 and Table S2). Similarly, also Tufted Duck populations have almost disappeared (see Table S2).

Between-species correlations based on the mean density in a given water body showed interesting patterns. Only two out of 36 pairwise correlations in waterfowl, diver, and grebe species were significant ($P < 0.05$, between mergansers, and between Eurasian Wigeon and Common Teal, Table 3) and none between the gull species (six pairwise correlations). In contrast, five of the 36 pairwise correlations between waterfowl, divers, grebes and gull species showed a significant positive pattern ($P < 0.05$): between Black-headed Gull and Pochard, Common Gull and Red-Breasted merganser, Common Gull and Common Merganser, Lesser Black-backed Gull and Black-throated Diver, and Herring Gull and Black-throated Diver.

Water clarity had decreased during the period (increase of turbidity and decrease of Secchi depth, Fig. 2). In a linear regression based on waterbird densities in western main Kukkia only (where the sample plot measuring water quality was located), turbidity (mean of the census year and the previous year) significantly explained density change of the declined ducks (all ducks except mallard; $r^2 = 0.928$, $F_{1,2} = 25.759$, $P = 0.037$), but not in grebes ($r^2 = 0.047$, $F_{1,2} = 0.100$, $P = 0.782$), in the Black-throated Diver ($r^2 = 0.739$, $F_{1,2} = 5.649$, $P = 0.141$) or in gulls ($r^2 = 0.221$, $F_{1,2} = 0.566$, $P = 0.530$).

A.

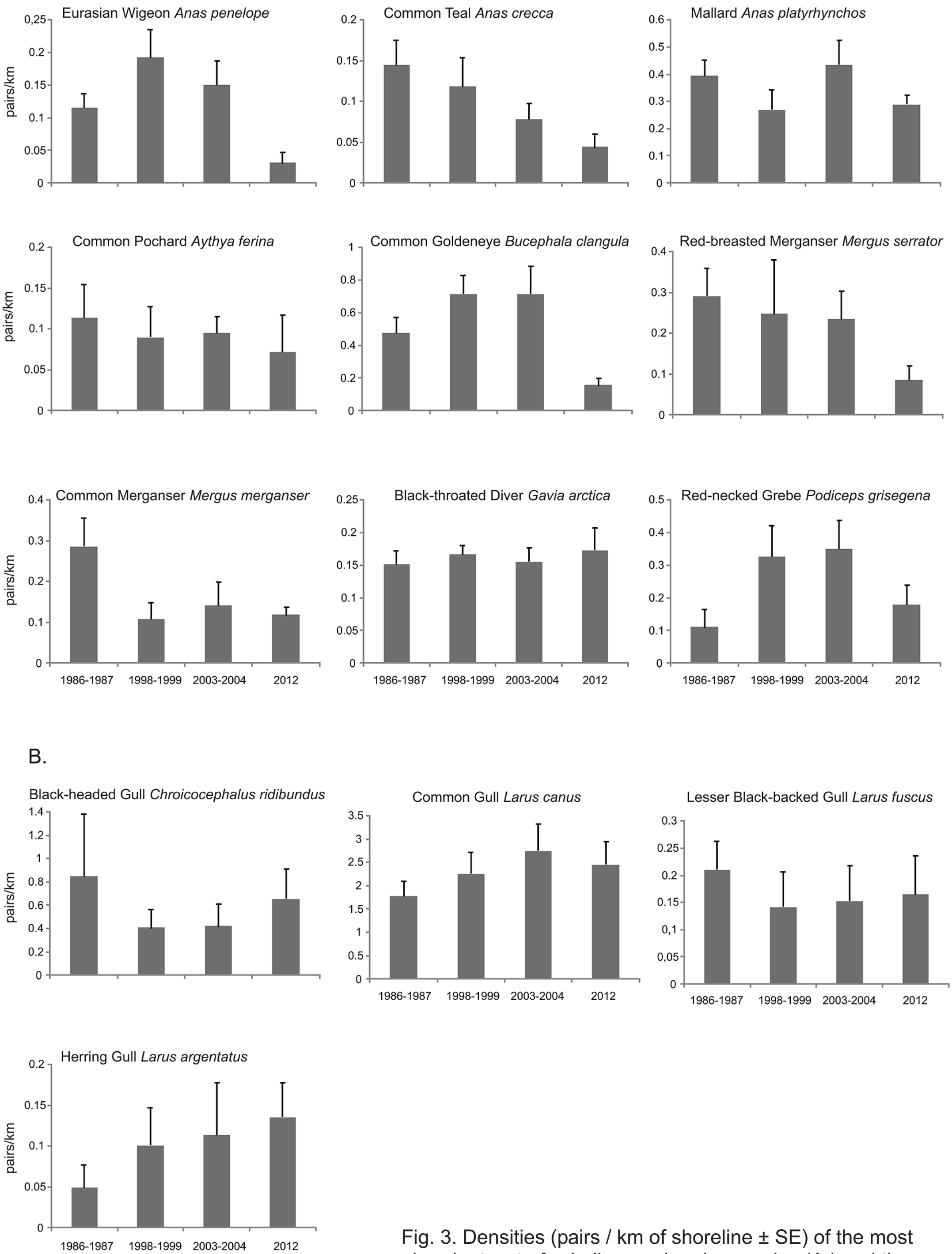

Fig. 3. Densities (pairs / km of shoreline ± SE) of the most abundant waterfowl, diver and grebe species (A.) and those of the gull species (B.) in the Kukkia lake complex between 1986 and 2012. Densities are here original values, which were log(x + 1) transformed for the analyses.

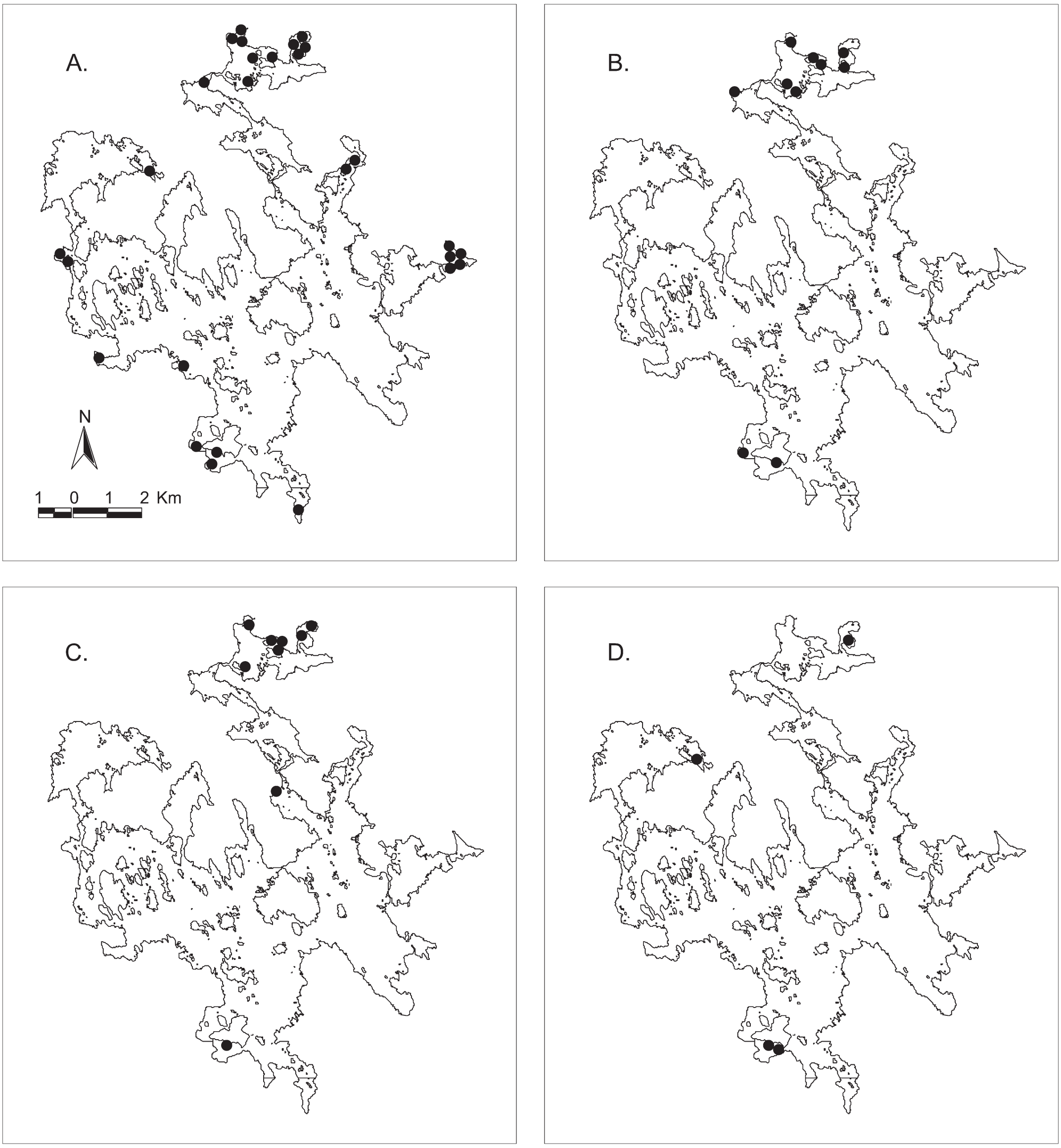

Fig. 4. Location of pairs (dots) of the Great Crested Grebe (*Podiceps cristatus*) in 1986–2012. A. = 1986–87, B. = 1998–99, C. = 2003–2004, D. = 2012. (National Land Survey of Finland, Permit number MML/VIR/TIPA/182/10).

4. Discussion

4.1. Population trends and spatial dynamics

Population changes in waterbirds observed in the present study are in line with the nationwide population trends of waterbirds (waterfowl, divers and grebes) in Finland in 1986–2011 (Pöysä *et al.* 2013), in which the present study data was not included. Pöysä *et al.* divided their study in two periods: 1986–1996 and 1997–2011, and population declines occurred particularly in the latter period. Also, in my study most of the population declines in waterbirds occurred between 2003/04 and 2012. Species declining nationwide in 1997–2011 included the Eurasian Wigeon, Common Golden-

Table 3. Pairwise correlations (Pearson correlation coefficient, r) in waterfowl, diver, grebe and gull species based on densities in the different water bodies. Abbreviations: Apen = *Anas penelope*, Acre = *A. crecca*, Apla = *A. platyrhynchos*, Afer = *Aythya ferina*, Bcla = *Bucephala clangula*, Mser = *Mergus serrator*, Mmer = *M. merganser*, Garc = *Gavia arctica*, Pgri = *Podiceps grisegena*, Crid = *Chroicocephalus ridibundus*, Lcan = *Larus canus*, Lfus = *L. fuscus*, Larg = *L. argentatus*. *N* = 7 in each case. Significant correlations: * (*P* < 0.05), ** (*P* < 0.01).

Species	Apen	Acre	Apla	Afer	Bcla	Mser	Mmer	Garc	Pgri	Crid	Lcan	Lfus
Acre	0.786*	–	–	–	–	–	–	–	–	–	–	–
Apla	–0.035	0.384	–	–	–	–	–	–	–	–	–	–
Afer	0.672	0.255	0.074	–	–	–	–	–	–	–	–	–
Bcla	0.525	0.568	0.536	0.534	–	–	–	–	–	–	–	–
Mser	–0.694	–0.525	0.227	–0.459	–0.019	–	–	–	–	–	–	–
Mmer	–0.406	0.006	0.448	–0.617	0.109	0.791*	–	–	–	–	–	–
Garc	–0.478	–0.234	0.559	–0.240	–0.262	0.267	0.332	–	–	–	–	–
Pgri	0.183	0.226	0.374	0.515	0.280	–0.443	–0.556	–0.022	–	–	–	–
Crid	0.656	0.173	–0.041	0.959**	0.557	–0.364	–0.541	–0.289	0.288	–	–	–
Lcan	–0.494	–0.204	0.564	–0.407	0.046	0.756*	0.846*	0.716	–0.462	–0.329	–	–
Lfus	–0.178	0.099	0.689	–0.105	0.086	0.102	0.344	0.895**	–0.028	–0.115	0.693	–
Larg	–0.417	0.173	0.102	–0.067	–0.560	0.179	0.041	0.825*	–0.135	–0.091	0.475	0.577

eye, Common Pochard, Common Merganser, Red-breasted Merganser, Great Crested Grebe and Red-necked Grebe, all of which also showed similar patterns in the Kukkia lake complex. In the Common Goldeneye and Red-necked Grebe, the temporal patterns were also similar in the longer term both nationwide and in Kukkia: first a significant increase and then a significant decrease.

The threat status of many waterbird species was raised from the Finnish Red-List evaluation of 2010 to that of 2015 (Rassi *et al.* 2010, Tiainen *et al.* 2016, e.g., in Eurasian Wigeon, Common Pochard, Tufted Duck, Red-Breasted Merganser, Common Merganser and Great Crested Grebe). According to the results of the present study this procedure was highly well-founded.

In contrast to waterfowl and grebes, gull populations did not decline, but remained stable (the Black-headed Gull and the Lesser Black-backed Gull) or slightly increased (the Common Gull and the Herring Gull). The increase of Herring Gull populations is due to the fact that the species utilizes dumps (the nearest situated at a distance of 40 km), which provide extra food, particularly in early spring. In the gulls there are large between-species differences in their spatial and temporal dynamics, so that the Common Gull showed very low spatial turnover in nesting sites whereas the Red-Listed Black-headed Gull and the Lesser Black-backed Gull had a much higher spatial turnover (Virkkala 2006). However, in the waterfowl and grebe species, the spatiotemporal density variation may even be higher than in the Red-Listed gulls.

The population density of species varied significantly between the water bodies, showing that waterbird species prefer certain water bodies within the lake system, and thus populations are not uniformly distributed between the waterbodies. Species were also distributed largely independently, because only two out of 42 of the pairwise correlations in waterfowl, diver and grebe and in gull species were significant. At the significance level of 0.05, two out of 40 comparisons would be expected to be significant merely for stochastic reasons. In contrast, there were more similarities in spatial patterns between waterfowl, divers, grebes and gulls, because five of the 36 pairwise correlations were significant and positive.

The positive correlation between the Black-headed Gull and the Common Pochard corroborates the fact that Common Pochards prefer to breed in or nearby Black-headed Gull colonies (see Väänänen 2000, Väänänen *et al*. 2016) due to decreased risk of predation. The other positive correlations between gulls and waterfowl and gulls and diver are probably more related to similar habitat and spatial preferences (e.g., Black-throated Diver – Lesser Black-backed Gull, Common Gull – Common Merganser).

4.2. Changes in water quality

Pöysä *et al.* (2013) analyzed different factors affecting population trends in waterbirds, including hunting pressure, life history characteristics (body mass and clutch size) and eutrophication. Neither hunting pressure nor life history characteristics seemed to explain the population trends, but the authors suggested that eutrophication reducing food availability for the waterbirds might cause the population decline in many waterbird species. Lehikoinen *et al.* (2016) showed that population trends of Eurasian Wigeon, Tufted Duck and Teal exhibited significantly negative long-term trends in eutrophic but not in oligotrophic wetlands and water areas in 1986–2013. They suggest that particularly over-eutrophication of already eutrophicated wetlands and water areas are a main threat to these species populations (see also Fox *et al.* 2015). In contrast, in the Common Goldeneye and Mallard no difference in the patterns of density trends between eutrophic and oligotrophic wetland were observed (Lehikoinen *et al.* 2016). However, only a few detailed analyses of the direct effect of overeutrophication on the population changes has been carried out. In a case study, Lehikoinen *et al.* (2016) showed that while open shore meadows, horsetail (*Equisetum fluviatile*) and submerged vegetation declined, numbers of Eurasian Wigeons and Tufted Ducks declined between 1989 and 2007. However, Lehikoinen *et al*. (2016) did not present any statistical analyses between the patterns of vegetation change and trends of these waterfowl species. Eutrophication has also been suggested as a cause of the declines of the Common Goldeneye in the Archipelago Sea of the Baltic Sea in Finland (Rönkä *et al.* 2005).

In the oligo-mesotrophic Kukkia lake complex there were signs of water quality deterioration, although no clear impact of eutrophication was observed. However, there was an increase in turbidity (and decrease in Secchi depth) showing that water clarity had decreased, and this change significantly explained the population change of declining ducks. Change in water quality affects fish-eating waterbirds using vision in catching prey (see e.g. Holopainen *et al.* 2015), and of the three species preferring oligotrophic lakes, two fish-eaters (Common Merganser and Red-breasted Merganser) did indeed decline in the Kukkia lake complex. Change in water quality probably also affects indirectly by change in fish composition (see Nummi *et al.* 2016 and references therein). Increase in turbidity favours e.g. Perch (*Perca fluviatilis*), which compete with Goldeneye (particularly broods) for the invertebrate food resources (Nummi *et al.* 2012). Thus, already even this change in water quality might considerably affect waterfowl species, and be harmful to the species preferring oligotrophic lakes (see also Kauppinen 1993).

On the other hand, of the three common species preferring eutrophic lakes, two declined (the Eurasian Wigeon and the Common Pochard), and the Red-necked Grebe showed a quadratic pattern (first increase and then decrease). In addition, the populations of the Great Crested Grebe and the Tufted Duck, which prefer eutrophic lakes, have collapsed in the Kukkia lake system. These results seem to be partly contrary to the hypothesis of eutrophication being the key driver in waterbird population trends. It should, however, be noted that the water bodies in the Kukkia lake complex are probably a suboptimal habitat for many of the species preferring eutrophic lakes (e.g., Eurasian Wigeon, Common Pochard, Tufted Duck, Great Crested Grebe), and it may well be that the decline of these species due to overeutrophication in their optimal habitats in eutrophic wetlands and water bodies (Pöysä *et al.* 2013, Lehikoinen *et al.* 2016) is also reflected in populations in their nearby suboptimal habitats in oligo-mesotrophic lakes, although at a national level population changes might not be as apparent in oligotrophic lakes.

4.3. Climate change

Climate change causes species to shift their ranges (Hickling *et al.* 2006, Huntley *et al.* 2007) and their densities (Virkkala & Lehikoinen 2014) northwards in Europe. Climate change-driven range shifts are projected to be most dramatic at northern latitudes because of the greater projected increases in temperature (Jetz *et al.* 2007). Boreal waterbirds have been observed to be highly responsive to climate warming with advancing migration in spring (Rainio *et al.* 2006) and delaying migration in autumn (Lehikoinen & Jaatinen 2012). Furthermore, wintering distributions of common waterfowl species (Tufted Duck, Common Goldeneye and Common Merganser) have shifted rapidly northwards in Northern Europe (Lehikoinen *et al.* 2013).

In Finland, the temperature has risen considerably from the 1980s (see Virkkala *et al.* 2014), having already caused bird species to shift their ranges and densities northwards so that, in particular, southern species have increased and enlarged their ranges and northern species have declined and retreated northwards (Virkkala & Rajasärkkä 2011, Brommer *et al.* 2012, Virkkala & Lehikoinen 2014). Of the waterfowl, diver and grebe species studied, six were northern, and only one of southern distribution in Europe. Five of the six northern species declined in the Kukkia lake complex situated in the southern boreal zone. However, the southern species, Common Pochard, has also declined. But nevertheless, climatic factors are important in defining species ranges at the biogeographic level, and changes in the climatic variables are reflected in the distribution and density of bird species (for ducks, see Guillemain *et al.* 2013, Fox *et al.* 2015). For example, in a study of factors affecting waterfowl populations, Kauppinen & Väänänen (1999) showed that weather variation both in the breeding and the wintering areas were significant in explaining population fluctuations of Garganey (*Anas querquedula*), Pintail (*A. acuta*), Common Goldeneye and Mallard. Pöysä & Väänänen (2014) showed that weather conditions during the spring migration largely drive interannual variation in Garganey numbers at the edge of the species' range.

4.4. Conservation implications

Some of the most abundant waterbird species populations have remained rather stable in the Kukkia lake complex, such as the Black-throated Diver or the Lesser Black-backed Gull, or even slightly increased, such as the Common Gull. However, almost all duck (all except the Mallard) species and both grebes have considerably declined in the early 21st century. The Common Goldeneye was earlier the second or third numerous waterbird species, but now its population has collapsed and the species is no longer among the seven most abundant waterbird species according to my study. Mallard is the only species of ducks, the population size of which has remained rather stable (see also Dalby *et al.* 2013). As newcomers during the study period, the Whooper Swan and the Canada Goose (*Branta canadensis*), have colonized Kukkia lake complex at the turn of the 20th and 21st century (See Table S2), and increased since then. Canada Goose is an introduced species, and seems to increase at present rapidly (own obs.). When all population changes of species are taken into account, the overall conservation value of waterbird community has declined, which is particularly worrying, because the Kukkia lake complex belongs also to the network of Important Bird Areas in Europe. The present legislation does not explicitly restrict the building of summer or permanent residencies on the shores of Natura 2000 area, of which water areas only are included to the Natura 2000 network. In addition, between-species interactions, such as the increase of introduced species via increased mammal predation (particularly the American Mink (*Neovison vison*)) or by the Canada Goose, may threaten many original waterbird species in the future.

Decrease in water quality with climate change probably is one of the key factors affecting population changes, but increased human disturbance due to further building of shorelines causes an additional threat. The negative effects of climate warming on breeding water and shore birds are best alleviated by reducing the nutrient load to water bodies in order to restrict the eutrophication (see Ekholm *et al.* 2007) and to protect properly and restore the optimal habitats for species (see Johnston *et al.* 2013, Bregnballe *et al.* 2014, Virkkala *et al.* 2014).

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Vesilintu- ja lokkikantojen ajalliset ja alueelliset muutokset boreaalisella järvikompleksilla

Vesilintu- ja lokkipopulaatioiden ajallisia ja alueellisia muutoksia tutkittiin boreaalisessa järvisysteemissä vuodesta 1986 vuoteen 2012. Tutkimus perustui kaikkien vesilintu- ja lokkilajien parien

laskentaan Kukkian järvikompleksissa, jonka pinta-ala on 45,75 km^2 ja rantaviivan pituus 290 km (mittakaava 1:20 000). Tuloksia verrattiin mm. muutoksiin veden laadussa tutkimusjakson aikana. Lajien kannantiheydet erosivat eri osa-alueiden välillä, joten lajit suosivat eri vesialueita järvikompleksissa. Monien vesilintu- ja lokkilajien alueellinen esiintyminen oli kuitenkin samankaltaista johtuen todennäköisesti lajien välisestä positiivisesta vuorovaikutussuhteesta (esim. naurulokki – punasotka) tai lajien samankaltaisesta elinympäristönvalinnasta (esim. kuikka – selkälokki).

Sorsa- ja uikkulajien kannat keskimäärin vähenivät tutkimusjakson aikana: seitsemällä kahdeksasta runsaimmasta lajista havaittiin joko negatiivinen lineaarinen tai epälineaarinen (ensin runsastuminen, sitten taantuminen) ajallinen kannanmuutos. Sorsalintujen kokonaisparimäärä pysyi aluksi vakaana mutta väheni sitten voimakkaasti noin puoleen aikajaksolla 2003/2004–2012. Sen sijaan kuikan kanta pysyi vakaana, ja kaksi neljästä lokkilajista (kalalokki ja harmaalokki) jopa runsastuivat tutkimusjakson aikana.

Veden kirkkaus heikkeni tutkimusvuosien aikana merkitsevästi, mikä voi olla yksi syy vesilintupopulaatioiden kantojen pienenemiseen, sillä sameuden lisääntyminen paljolti selitti vähentyneiden sorsalintujen negatiivista populaatiotrendiä. Ilmastonmuutos lisää rehevöitymistä ja vesien samentumista, millä voi olla negatiivinen vaikutus vesilintupopulaatioihin.

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Online supplementary material

Table S1. Characteristics of the water bodies of the Kukkia lake complex.
Table S2. Number of bird pairs observed in the total lake complex in the study years.
Table S3. Status of the most abundant species studie in different classifications.