

1 **Effects of flyway-wide weather conditions and breeding habitat on the breeding abundance of**
2 **migratory boreal waterbirds**

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11 climate and habitat

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22 ABSTRACT

23 Anthropogenic habitat loss and climate change are among the major threats to biodiversity.
24 Bioclimatic zones such as the boreal and arctic regions are undergoing rapid environmental change,
25 which will likely trigger changes in wildlife communities. Disentangling the effects of different
26 drivers of environmental change on species is fundamental to better understand population dynamics
27 under changing conditions. Therefore, in this study we investigate the synergistic effect of winter and
28 summer weather conditions and habitat type on the abundance of 17 migratory boreal waterbird
29 species breeding in Finland using three decades (1986–2015) of count data. We found that above-
30 average temperatures and precipitations across the western and northern range of the wintering
31 grounds have a positive impact on breeding numbers in the following season, particularly for
32 waterbirds breeding in eutrophic wetlands. Conversely, summer temperatures did not seem to affect
33 waterbird abundance. Moreover, waterbird abundance was higher in eutrophic than in oligotrophic
34 wetlands, but long term trends indicated that populations are decreasing faster in eutrophic than in
35 oligotrophic wetlands. Our results suggest that global warming may apparently benefit waterbirds,
36 e.g. by increased winter survival due to more favourable winter weather conditions. However, the
37 observed population declines, particularly in eutrophic wetlands, may also indicate that the quality of
38 breeding habitat is rapidly deteriorating through increased eutrophication in Finland which override
39 the climatic effects. The findings of this study highlight the importance of embracing a holistic
40 approach, from the level of a single catchment up to the whole flyway, in order to effectively address
41 the threats that waterbirds face on their breeding as well as wintering grounds.

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46 INTRODUCTION

47 Understanding how global environmental change affects abundance and population dynamics of
48 wildlife is a core topic in ecology and conservation biology (e.g. Begon et al. 1994) and has been
49 widely studied in the past century. The rapid and continuous human-induced alteration of the majority
50 of Earth's ecosystems has been indicated as the most important cause of the global biodiversity loss
51 (e.g. Pimm et al. 2006). However, evidence is accumulating that climate change is becoming a major
52 threat for most taxa (Parmesan 2006, Thomas and Williamson 2012). Even though the future global
53 climate scenarios are bound with uncertainty, changes in climate to date have gone beyond the
54 expected natural variability (IPCC 2013). Furthermore, the climate is not changing at the same speed
55 and direction across the globe, with the arctic and boreal zones undergoing the fastest changes (IPCC
56 2012, 2013).

57 Climate change can affect species by directly modifying their physical environment, e.g. through
58 variation in temperature that may trigger toxic algal and cyanobacteria blooms, loss of food and
59 protection resources (i.e. underwater vegetation) and outbreaks of diseases such as botulism (Moss et
60 al. 2011). In addition, climate change can also trigger changes in inter-specific interactions such as
61 competition for resources, host-parasite interactions and predator-prey dynamics (Parmesan 2006).
62 In this context, species that inhabit bioclimatic regions undergoing rapid climate change during, at
63 least, part of their life cycle are thought to be at greatest risk from rapidly changing climatic conditions
64 (Gonzalez et al. 2010) but also from continuous habitat transformation (Stoate et al. 2009).
65 Furthermore, aquatic ecosystems are especially threatened by climate change (Moss et al. 2011,
66 Guareschi et al. 2015), which may accelerate the speed at which wetland dependent species lose their
67 optimal habitat. These species may thus be in urgent need for adaptive conservation actions (e.g.
68 Mawdsley 2011). However developing conservation measures for species threatened by climate
69 change is not a trivial task, particularly for bird species breeding in the arctic and boreal regions, as
70 most of them are migratory, spending different phases of their annual cycle in various bioclimatic

71 zones of the planet. Migratory species may be more vulnerable to climate change because of the
72 differential speed and severity of changes in climate in different areas where they occur throughout
73 the annual cycle. This may increase the risk of phenological mismatches (Knudsen et al. 2011, Pearce-
74 Higgins and Green 2014).

75 The majority of waterbird species breeding in the arctic and boreal regions are predicted to suffer the
76 most from climate change during the breeding season but also throughout the entire annual cycle
77 (Guillemain et al. 2013, Fox et al. 2015, Lehikoinen et al. 2016a, b). However, it has been shown that
78 waterbirds are highly responsive to changes in weather conditions as compared to other groups of
79 birds (Brommer 2008). Specifically, waterbirds seem to be able to shift their wintering (Zipkin et al.
80 2010, Lehikoinen et al. 2013) and breeding (e.g. Østenes and Kroglund 2015) distributions and/or to
81 modify their phenology (Rainio et al. 2006, Hansson et al. 2014) in response to climate change. Given
82 their high ecological, economic and societal value, coupled with their widespread population declines
83 owing to habitat loss and climate change, waterbirds constitute a group of species of high
84 conservation concern (Green and Elmberg 2014, Guareschi et al. 2015). As a result, most waterbird
85 species and their key habitats are nowadays protected under international legislation and agreements,
86 such as the Convention on Migratory Species (CMS), the RAMSAR Convention, African-Eurasian
87 Waterbird Agreement (AEWA) and the Natura2000 network under the EU Birds Directive and the
88 EU Habitats Directive. However, effective evidence-based conservation can only be achieved if
89 fundamental ecological knowledge such as the drivers of change in populations, is available
90 (Courchamp et al. 2015). For waterbirds in particular, a good understanding of the drivers of change
91 across their annual cycle is often lacking. Hence, disentangling the effects of habitat type and quality
92 and climatic conditions on waterbird population dynamics can yield knowledge relevant for designing
93 new or adjust existing conservation measures.

94 Here we use a long-term dataset to study how different drivers of environmental change affect
95 population dynamics of waterbirds breeding in the boreal region of Europe. In particular, we assess

96 the effect of weather conditions during the breeding and the wintering season on the combined
97 abundance of 17 migratory waterbird species breeding in Finland in the past three decades. We also
98 investigate whether such climatic effects differ between three contrasting breeding habitat types: (1)
99 oligotrophic wetlands, (2) naturally eutrophic wetlands and (3) human-influenced wetlands
100 surrounded by agricultural landscapes and urban areas with large nutrient load. We predict that mild
101 weather conditions during winter increase waterbird numbers recorded during the following breeding
102 season through improved survival (Guillemain et al. 2013, Gunnarsson et al. 2012). Furthermore,
103 increasing temperature in summer should improve breeding success (Fox et al. 2015), thereby
104 contributing to increased breeding numbers with one year lag. However, these impacts of climatic
105 conditions may be conditional to the type of breeding habitat, which may potentiate or counteract the
106 climatic effects. Last, we predict that, in general, trends in breeding waterbird numbers will differ by
107 habitat type, with more negative trends in habitats with higher nutrient load (wetlands in
108 agricultural/urban areas) than in oligotrophic wetlands due to hyper-eutrophication process (e.g. Moss
109 et al. 2011), as also previously shown by Lehikoinen et al. (2016b). Our study provides one of the
110 very few examples where impacts of climatic and other environmental variables, and their
111 interactions, have been simultaneously considered. We believe that the evidence provided here could
112 help to guide international conservation measures in the context of climate change adaptation and
113 hunting regulations, and ultimately ensure the long-term viability of waterbird populations.

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115 METHODS

116 *Waterbird count data*

117 Here we use a long-term (1986–2015) dataset on waterbird breeding abundance in Finland. Overall,
118 110 077 breeding pairs of 17 migratory species of waterbirds were counted in the 30 years of study
119 (see Supplementary Material Appendix 1 Table A1 for details). Although all 17 species are regular

120 breeders in Finland (Valkama et al. 2011), there are substantial differences in abundance (i.e. breeding
121 population) between them and also large inter-annual variation in breeding numbers within species.

122 The breeding waterbird census in Finland has been coordinated by the Finnish Museum of Natural
123 History since 1986. This census consists of two visits to each surveyed wetland per year. A first visit
124 is carried out in early May and a second visit in late May in order to account for the different timing
125 between early (e.g. mallard, common pochard and common goldeneye) and late (e.g. Eurasian
126 wigeon, tufted duck, red-breasted merganser) breeding species. Hence, for this study, we used only
127 count data derived from the first visit for the early breeding species, and only from the second visit
128 for the late breeding species within each year. Each census is carried out by experienced volunteer
129 bird watchers which are assigned a route or several wetlands to be surveyed (the detailed census
130 method is described in Koskimies and Väisänen [1991]).

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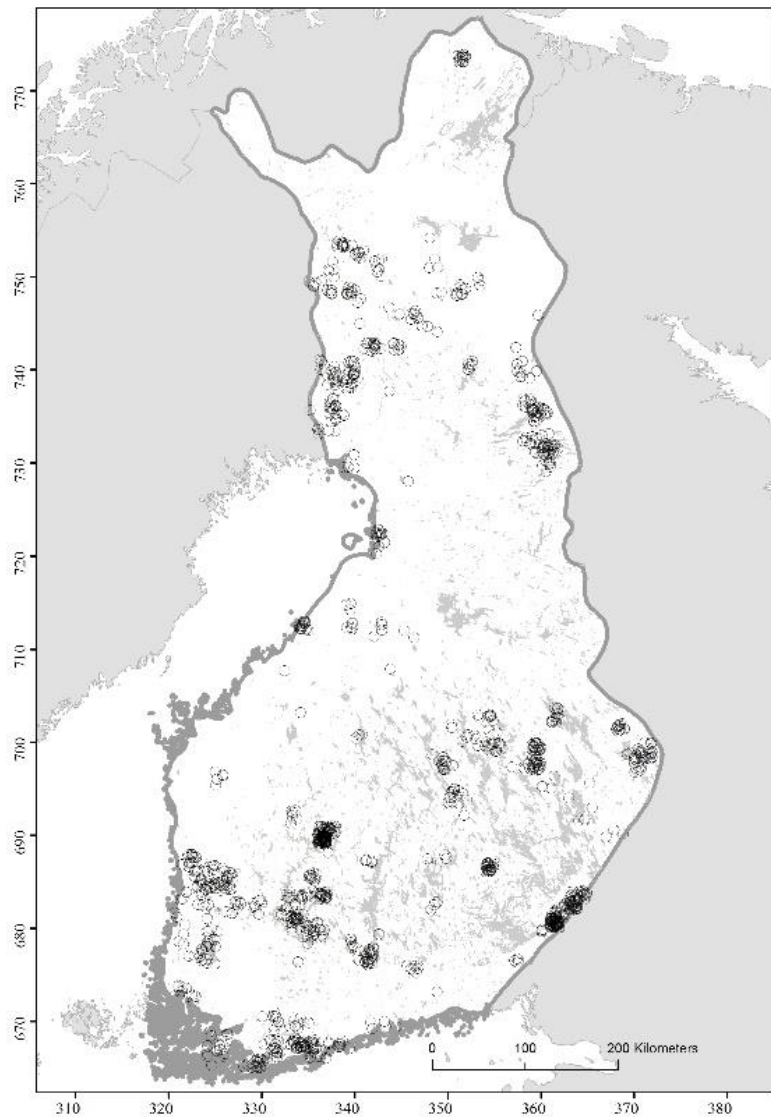
132 *Habitat data*

133 The census sites include wetlands of varying sizes and with different levels of nutrient load. All
134 wetlands are originally classified into eight habitat categories (see Lehtikoinen et al. 2016b for a
135 complete description of the eight categories), but for the purpose of this study we merged these
136 categories, resulting in three habitat classes: (1) oligotrophic wetlands with no vegetation, (2)
137 naturally eutrophic wetlands surrounded by forests, peatlands or reed beds and (3) eutrophic wetlands
138 surrounded by agricultural land or urban areas where the eutrophication process has been at least
139 partly caused by human actions. The merging was done in order to reduce model complexity and
140 make results more easily interpretable while retaining biologically meaningful habitat categories.

141 Although the habitat classification that we used here refers to the physical characteristics of the
142 wetlands, these could be seen, to some extent, as different levels of habitat quality (Lehtikoinen et al.
143 2016b). In this sense, the habitat quality would be highest in oligotrophic wetlands, intermediate in

144 naturally eutrophic and lowest quality in wetlands surrounded by farmland and urban areas due to
145 high levels of human pressure and disturbance as well as potentially high levels of eutrophication.

146 The study sites included in the
147 Finnish breeding waterbird census
148 scheme are distributed across
149 Finland, covering a large latitudinal
150 gradient (Fig. 1). For the purpose of
151 this study, we selected wetlands that
152 were surveyed more than 2 years
153 since the start of the monitoring
154 scheme in 1986 (n = 1280
155 wetlands). Not all selected sites
156 were monitored every year (range
157 110–873 monitored sites per year)
158 but the number of censused sites
159 was relatively balanced over the
160 study period (Supplementary
161 Material Appendix 1, Fig. A1). All



162 censuses are carried out well before
163 the reed beds cover the shores to ensure optimal visibility during the census, thereby maximizing
164 detectability. The size (hectares) of each wetland was calculated *a posteriori* using GIS tools.

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Figure 1. Location of the 1280 wetlands surveyed during the study period (1986 – 2015).

168 *Weather data*

169 The winter North Atlantic Oscillation Index (hereafter NAOI) was used in this study as a proxy for
170 the general winter weather conditions that the waterbirds considered in this study face across their
171 main wintering areas. The NAOI is calculated as the difference between the normalized sea level
172 pressures in Reykjavik (Iceland) and Lisbon (Portugal) since 1864 (Hurrell et al. 2016). In general,
173 positive values of NAOI are associated with higher temperature and precipitation during winter than
174 average in western and northern Europe. Positive values of NAOI are also associated with above-
175 average rainfall in northern Europe in winter, but also to drier than average winters in southern
176 Europe. The opposite pattern is true for negative values of NAOI (Hurrell et al. 2016). Monthly NAOI
177 data related to Western Europe were downloaded from
178 <http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>. In order to obtain a single
179 value for the “general conditions of the winter in western Europe” prior to the breeding season, we
180 averaged the NAOI values of December, January and February each winter.

181 As a measure of general summer weather conditions, we downloaded June temperature from 1986 to
182 2013 for the two 5° x 5° grids covering most of Finland (available at the Climate Research Unit of
183 the University of East Anglia’s website: <http://www.cru.uea.ac.uk/>). The June temperature values for
184 each year in both grids (see above) were then averaged to obtain a single June temperature value per
185 year. Because we assume that summer weather conditions mainly affect breeding success, we can
186 expect breeding numbers in a given year to be linked to the amount of recruits of young individuals
187 from the previous breeding season, survival of which may be also affected by summer weather
188 conditions during the fledgling period (Koskimies and Lahti 1964, Steen et al. 2014, Arzel et al.
189 2015). In Finland, the brood-rearing phase of most species occurs during June (e.g. Oja and Pöysä
190 2007, Arzel et al. 2015). Therefore we decided to model the waterbird counts in year t as a function
191 of summer weather conditions in the preceding year, $t-1$. That is, we related breeding waterbird

192 abundance in year, e.g. 1991, to weather conditions in summer (mean June temperature) 1990 (see
193 Lehtikoinen et al. 2016a).

194

195 *Interactions*

196 We included three two-way interactions in our model (see below) to assess three different processes
197 that may be important for waterbird population dynamics. It has been shown that population trends
198 of several species of waterbirds breeding in Finland differ depending on the type of habitat they use
199 for breeding (oligotrophic vs. eutrophic; Lehtikoinen et al. 2016b). We took this comparison one step
200 further by creating a three-categories habitat variable, differentiating naturally eutrophic wetlands
201 from those under large anthropogenic impacts close to urban and farmland areas. Hence, we defined
202 an interaction to quantify different population trends over time in the three habitat types ('year' ×
203 'habitat type'). Second, we wanted to investigate whether the impact of weather conditions on
204 breeding numbers differed between habitats. Because we considered two weather variables relating
205 to winter and summer weather conditions, we defined two interactions to quantify whether possible
206 effects of these two weather variables on breeding numbers differ according to the habitat type where
207 birds have been found breeding (i.e. 'winter weather conditions' × 'habitat type' and 'summer
208 temperature' × 'habitat type').

209

210 *Statistical analysis*

211 Our main aim was to assess the effects of winter and summer weather conditions, habitat type, and
212 the interaction of weather and habitat on the combined abundance of 17 migratory waterbird species
213 breeding in Finland. Due to the nature of our data, we *a priori* expected to find large variation in the
214 count data within and between species, as well as a large number of zeroes (i.e. several wetlands per
215 year where a species was not observed, zero inflation). As expected, the dispersion statistic (e.g. Zuur

216 and Ieno 2016a, b) of the *Poisson* Generalized Linear Mixed Models (GLMM) fitted to the data
 217 showed that the model was overdispersed. Hence, we fitted the next model in complexity, a *Negative*
 218 *Binomial* GLMM (see Zuur and Ieno 2016a). This provided a good fit after checking for
 219 overdispersion, heterogeneity and residual patterns and non-linearity (see Zuur et al. 2009, 2010, Zuur
 220 and Ieno 2016a). Thus, there was no need to fit a zero-inflated model. To account for different
 221 correlation structures in our data, we defined ‘Year’ as a random term (we have several observations
 222 each year and those observation within the same year are likely to be more similar than observations
 223 between years). In addition, we defined a random effect of ‘Species’ nested within ‘Site’ (we have
 224 multiple observations from the same site and many species per site). Following the recommendations
 225 by Zuur and Ieno (2016b), the mathematical notation for the statistical model fitted (crossed and
 226 nested GLMM *NB*) is denoted as follows:

$$227 \text{ Count}_i \sim NB(\mu_i, K)$$

$$228 E(\text{Count}_i) = \mu_i \quad \text{and} \quad \text{var}(\text{Count}_i) = \mu_i + \mu_i^2 \div K$$

$$229 \mu_i = e^{\eta_i}$$

$$230 \eta_{i,j,k,l} = W_{i,j,k,l} + S_{i,j,k,l} + H_j + Year_{i,j,k,l} + Year_{i,j,k,l}^2 + Count_{i,j,k,l-1} + X_j + Y_j$$

$$231 \quad + W_{i,j,k,l} \times H_j + S_{i,j,k,l} \times H_j + Year_{i,j,k,l} \times H_j + Year_l + Site_j + Species_k$$

232 (eqn.1)

$$233 Year_l \sim N(0, \sigma_{year}^2)$$

$$234 Site_j \sim N(0, \sigma_{site}^2)$$

$$235 Species_k \sim N(0, \sigma_{species}^2)$$

236

237 Where $\eta_{i,j,k,l}$ is the i^{th} observation (number of breeding pairs) of species k in site j in year l . W is the
238 NAOI value for winter and S represents the weather conditions during the preceding summer. $Year$
239 and $Year^2$ are continuous variables depicting linear and quadratic trends in counts over the study
240 period, because such trends have been shown by earlier studies (Pöysä et al. 2013, Lehikoinen et al.
241 2016b). H_j is the habitat type in site j . $Count$ is the autoregressive (AR) term (log-transformed count
242 of breeding pairs of species k in site j the preceding breeding season, $l-1$) to account for potential
243 temporal autocorrelation and density dependence. X and Y depict the longitude and latitude of site j
244 to account for potential spatial patterns.

245 The main objective of this study was first, to assess the overall effect of weather and habitat variables
246 on the breeding abundance of waterbirds (i.e. main effects) and, second, to assess the joint effect of
247 weather and habitat on the abundance (i.e. interactions). Therefore, our modelling approach consisted
248 in two steps: first, we ran the model in (eqn. 1) without the interactions to assess the overall effects
249 of the covariates that are included in the interactions in the model in (eqn. 1). Second, we ran the
250 model in (eqn. 1) to assess the effect of the interactions. After running the model in (eqn.1), we
251 proceeded with model selection only on the interactions (i.e. only interactions were dropped from the
252 full model if non-significant until all the remaining interactions in the model were significant; Bolker
253 2008, Bolker et al. 2008, Zuur and Ieno 2016b). We did this in order to be able to interpret correctly
254 the main effects of the covariates when the interactions were non-significant (Burnham and Anderson
255 2002, Arnold 2010).

256 All models were fitted using the package `glmmTMB` (Magnusson et al. 2016) in R.3.2.3 (R Core Team
257 2015). All continuous covariates were standardized (zero mean, unit standard deviation) in order to
258 make all coefficients comparable and to reduce correlation between linear and quadratic effects of
259 the covariate 'Year'. Collinearity among the covariates was assessed using the Variance Inflation
260 Factor (VIF) analysis. All VIF values were well below the threshold of three, suggesting low
261 collinearity among them (Zuur et al. 2009). We also inspected spatial correlograms based on the

262 model residuals (Zuur et al. 2009) in order to detect any sign of spatial autocorrelation
263 (Supplementary Material Appendix 1, figs. A2). We applied a similar procedure using autocorrelation
264 function (ACF) to detect any sign of temporal autocorrelation (Zuur et al. 2010) in the residuals. No
265 signs of spatial or temporal autocorrelation were detected in the residuals of the model.

266

267 RESULTS

268 The model explaining abundance of waterbirds breeding in Finland indicates that, among the weather
269 variables, winter NAO have an overall strong positive effect on waterbird numbers during the
270 following breeding season (mean estimate and SE = 0.035 ± 0.005 , $Z = 6.77$, $p < 0.001$; statistics
271 derived from a model where only main effects were included; see methods above). Conversely,
272 summer temperatures were found to have no overall effect on breeding waterbird abundance recorded
273 in Finland during the following year (mean estimate and SE = -0.003 ± 0.005 , $Z = -0.54$, $p = 0.59$;
274 statistics derived from a model where only main effects were included). As expected, we found that
275 abundance of breeding waterbirds in one year is positively related to the abundance in the preceding
276 year, and also positively related to the size of the wetland (i.e. the larger the wetland, the greater the
277 abundance; see Table 1). Across Finland, abundance of breeding waterbirds was highest towards the
278 east of the country (Table 1), and was also higher in the two habitats with high nutrient load as
279 compared to oligotrophic wetlands (mean estimate and SE for ‘naturally eutrophic wetlands’ =
280 1.039 ± 0.043 , $Z = 23.85$, $p < 0.001$; and mean estimate and SE for ‘eutrophic wetlands surrounded
281 by agricultural/urban areas = 1.199 ± 0.046 , $Z = 25.83$, $p < 0.001$; statistics derived from a model
282 where only main effects were included). While breeding waterbird numbers have been generally
283 declining across Finland, this decline was typically non-linear with a particularly severe drop in
284 numbers during the most recent years (mean estimate and SE = -0.039 ± 0.010 , $Z = -4.08$, $p < 0.001$;
285 statistics derived from a model where only main effects were included).

286 Interestingly, we found evidence that the impact of winter conditions and the population trends differ
 287 according to the main habitat type where the birds are found breeding (see significant interactions in
 288 Table 1).

289

290 **Table 1.** Estimated regression parameters, standard errors, z-values and P-values for the *NB* GLMM
 291 presented in eqn (1) after performing model selection on the non-significant interaction*. ‘Habitat’ is
 292 a categorical covariate with three levels (see methods). Here we present the results using the
 293 oligotrophic habitat type as a base level and the P-values showed are the corrections for the intercept
 294 for the other two habitat types (see e.g. Zuur and Ieno 2016b). The same applies to the interactions.

	Estimate	Std. Error	z value	P-value
Intercept	-3.740	0.710	-5.270	<0.001
Winter weather	-0.002	0.015	-0.140	0.893
Summer weather	-0.002	0.005	-0.410	0.680
Year	-0.046	0.024	-1.940	0.053
Year ²	-0.039	0.010	-4.100	<0.001
Habitat (naturally eutrophic)	1.016	0.045	22.470	< 0.001
Habitat (surrounded by agri/urban)	1.173	0.048	24.530	< 0.001
Wetland Size	0.502	0.020	25.200	< 0.001
Count preceding year	0.218	0.005	42.210	< 0.001
Latitude	-1.193	0.645	-1.850	0.064
Longitude	3.926	1.192	3.290	0.001
Winter : Habitat (naturally eutrophic)	0.045	0.018	2.600	0.009
Winter : Habitat (surrounded by agri/urban)	0.038	0.016	2.280	0.023
Year : Habitat (naturally eutrophic)	-0.022	0.027	-0.840	0.403
Year : Habitat (surrounded by agri/urban)	-0.065	0.026	-2.510	0.012
Summer : Habitat (naturally eutrophic)	0.019	0.017	1.120	0.261
Summer : Habitat (surrounded by agri/urban)	0.031	0.017	1.790	0.073

295 * Note that we also show the estimated regression parameter, standard error, z-values and P-values for the non-significant
 296 interaction between ‘Summer weather’ and ‘Habitat’ (see Zuur and Ieno 2016b), extracted from the full model showed in
 297 (eqn. 1) before performing model selection (see methods).

298

299 Specifically, effects of winter weather conditions were more positive for the fraction of the waterbird
 300 population breeding in naturally eutrophic wetlands and wetlands surrounded by agricultural land and
 301 urban areas compared to populations breeding in oligotrophic wetlands (interaction between winter

302 weather and habitat in Table 1). Moreover long-term population trends were significantly more
303 negative for the fraction of the population breeding in wetlands surrounded by agricultural land and
304 urban areas compared to that breeding in oligotrophic and naturally eutrophic wetlands (see the
305 interaction between year and habitat type in Table 1).

306

307 DISCUSSION

308 Here we provide strong evidence of the impact of winter weather conditions throughout the flyway
309 on boreal waterbird numbers breeding at high latitudes in Europe. We also show that the impact of
310 winter weather has a different magnitude according the habitat type which waterbirds use for
311 breeding. In addition, breeding waterbird numbers recorded in Finland are highest in the south and
312 east of the country, and in large sized wetlands. Results also indicate that breeding waterbirds have
313 been generally declining in Finland, with the magnitude of this decline being particularly important
314 in eutrophic wetlands surrounded by agricultural land and urban areas that currently support the
315 largest populations of breeding waterbirds. We believe that the observed declines are true population
316 declines and not caused by shifts in species populations as has been observed during wintering season
317 (Lehikoinen et al. 2013, Pavon-Jordan et al. 2015). It is unlikely that large number of birds would
318 have moved to breed outside Finland because breeding ducks are typically site faithful to their
319 breeding areas (Dow & Fredga 1983, Öst et al. 2012, Saurola et al. 2013, our results positive
320 autoregressive term). In addition, Finnish breeding bird atlas from the same study period suggest that
321 11 of our study species have shifted their distribution on average 24 kilometres northwards, which is
322 a similar rate of shift as in other bird species (Brommer et al. 2011).

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324

325

326 *Weather impacts on waterbird numbers by habitat type*

327 The result that breeding waterbird numbers are highest after winters with above-average temperature
328 and rainfall in western and northern Europe and drier than average in southern Europe (conditions
329 depicted by high NAOI values) largely matches our expectations. Moreover, the largest positive effect
330 of winter weather on waterbirds breeding in naturally eutrophic wetlands has also biological sense
331 and conservation implications. Drier winters in southern Europe may potentially reduce the quality
332 and availability of wetland habitats used by many wintering waterbirds (Gordo et al. 2011). However,
333 alongside a possible habitat deterioration in southern Europe (Rendón et al. 2008, Longoni 2010,
334 Márquez-Ferrando et al. 2014), the concomitant wet and mild conditions in western and northern
335 Europe may represent optimal conditions for wintering waterbirds that could largely counterbalance
336 the possible negative impacts of changed climate in southern Europe. Furthermore, the core wintering
337 area of most of our study species winter is located in western Europe and only a smaller proportion
338 of the population wintering in southern Europe (Wetlands International 2012, Fox et al. 2016).

339 The simultaneous changes in winter towards wet and mild conditions in Northern Europe may play a
340 synergistic role in enhancing winter survival of waterbirds. While above-average precipitation in
341 winter may increase habitat availability (Rendón et al. 2008), above-average temperatures may favour
342 the use of such increased habitat by boreal waterbirds that would have otherwise retreated further
343 south in Europe (Guillemain et al. 2013, Fox et al. 2015). Wetlands in northern Europe were
344 completely frozen up to few decades ago but are now largely ice-free and available for overwintering
345 waterbirds (Lehikoinen et al. 2013, Fox et al. 2015, Pavón-Jordán et al. 2015). Overall, suitable winter
346 conditions in Northern and western Europe may allow waterbirds to shorten their migration distance,
347 reduce energetic costs for thermoregulation and migration, and initiated breeding earlier and in better
348 body condition. The assertion above closely matches our results of a positive impact of mild winter
349 weather conditions (i.e. high NAOI values; above-average temperature and precipitation) on breeding
350 numbers. Other studies reported that reduced migration distances can increase waterbirds' over-

351 winter survival due to reduced movement costs and decreased intra- and inter-specific competition
352 for food resources, resulting in better foraging opportunities (Elmberg et al. 2014). Moreover, mild
353 winter weather was also associated with decreased thermoregulatory costs (Guillemain et al. 2013,
354 Dalby et al. 2013, Fox et al. 2015), with improved body condition before spring migration
355 (Guillemain et al. 2010, Fox and Walsh 2012), earlier departure from the wintering sites (Gordo 2007,
356 Knudsen et al. 2011, Donnelly et al. 2015) and potentially earlier arrival to the breeding grounds by
357 waterbirds (Murphy-Klassen et al. 2005, Rainio et al. 2006, Arzel et al. 2014, Chambers et al. 2014).

358 The stronger positive impact of improved winter weather conditions on birds breeding in eutrophic
359 wetlands is interesting. Waterbird populations in eutrophic wetlands are declining at a steeper pace
360 compared to those in oligotrophic wetlands, suggesting that the quality of eutrophic wetlands in
361 Finland may be rapidly deteriorating (see discussion below). As a result, the positive effect of
362 improved winter weather may become most manifest for those populations breeding in an already
363 poor quality habitat, such as eutrophic wetlands. Conversely, improved winter weather conditions
364 may only represent a marginal benefit, and thus unnoticeable statistically, for waterbird populations
365 breeding in a somewhat stable habitat type in terms of trends in quality, as represented by the
366 oligotrophic wetlands in this study.

367

368 *Waterbird abundance and trends by habitat type*

369 The observed population decline of waterbirds, particularly those breeding in eutrophic wetlands
370 surrounded by farmland and urban areas, sounds alarming for the conservation of this important guild.
371 This is particularly so given that eutrophic wetlands support the highest waterbird numbers in Finland.
372 The declining trend may sound apparently contradictory within the current global warming context;
373 favourable winter weather conditions in large parts of their range may benefit waterbirds (see above),
374 and yet population trends are negative, particularly in eutrophic wetlands. Therefore, it is most likely

375 that other environmental and anthropogenic factors (see below) may counterbalance the positive
376 impacts from recent years 'favourable' climatic conditions and drive the decline of breeding
377 waterbirds in Finland.

378 Our findings support those of previous studies highlighting the deteriorating state of waterbird
379 populations breeding in Finland (Pöysä et al. 2013, Lehikoinen et al. 2016b) and add the differential
380 dynamics of waterbird populations in naturally eutrophic wetlands and those eutrophic wetlands
381 surrounded by agricultural landscapes and urban areas which may be reaching a state of hyper-
382 eutrophication. Traditionally, naturally eutrophic lakes represented a preferred habitat for many
383 waterbirds in northern Europe, hosting higher species richness than oligotrophic lakes (Nilsson and
384 Nilsson 1978, Kauppinen and Väisänen 1993). However, eutrophic wetlands suitable for breeding
385 waterbirds may be disappearing in Finland and/or their quality may be deteriorating, especially those
386 in human-dominated landscapes, therefore causing the habitat specific population declines reported
387 here and also in previous studies (Pöysä et al. 2013, 2014, Fox et al. 2015, Lehikoinen et al. 2016b).

388 Although our results suggest that climate change may improve waterbird winter survival, it may also
389 trigger a deterioration in habitat quality in northern areas. This is because increasing winter
390 temperatures also cause an increase in rainfall, which in turn increases nutrient flow from the
391 catchment areas of farmland landscapes (Meier et al. 2012). This phenomenon is further exacerbated
392 by the increasing intensification of farming practices that typically implies, among others, an
393 increased use of inorganic fertilisers, as well as autumn ploughing and removal of edge vegetation,
394 all practices that facilitate runoff (Robinson and Sutherland 2002). The above practices, coupled with
395 increased precipitation patterns under climate change, may ultimately boost wetland over-
396 eutrophication. Moreover, eutrophication process may improve fish populations (Moss et al. 2011)
397 leading into increased competition between ducks and fish (Nummi et al. 2016).

398 On the other hand, increasing summer temperatures may cause an increase in algal biomass and
399 cyanobacteria, as well as in the amount of nutrients due to mineralization (Moss et al. 2011). Both of

400 these can lead to increasing eutrophication of wetlands, which is a symptom of severe habitat
401 degradation (Moss et al. 2011).

402

403 *Conclusions*

404 The importance of Finnish breeding grounds for European waterbirds is disproportionately high, with
405 the country supporting over half of the total European Union's populations of several waterbird
406 species, such as the northern pintail, common goldeneye, Eurasian wigeon and goosander (BirdLife
407 International 2015). Our results, by providing new insights into the synergistic effects of drivers of
408 change in populations of breeding waterbirds, have important implications for the conservation of
409 this guild not only in Finland but throughout their entire flyway.

410 This finding calls for a holistic approach for conserving such an important taxonomic group. While
411 management actions have been proved effective in restoring wetlands for waterbirds in different
412 regions (Giles 1994, Ma et al. 2010, Clausen et al. 2013, Bregnballe et al. 2014), our study suggests
413 that these may not be enough in Finnish boreal wetlands, especially in light of future climate change.
414 Conservation efforts should be targeted towards landscape level management measures that would
415 consider the whole catchment system rather than the sole waterbody area. These efforts, however,
416 may still be insufficient if implemented by a single country. As our study highlights, drivers of change
417 in waterbird populations act at different spatial scales and some span far beyond their breeding
418 grounds. Ultimately, international cooperation will be key for implementing evidence-based and
419 effective conservation measures to ensure that habitat for waterbirds is preserved according to the
420 current and future conditions dictated by climate change (Pavón-Jordán et al. 2015).

421

422

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