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Comparison of breeding bird trends between the Netherlands and Europe

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ABSTRACT

Capsule: Bird trends in the Netherlands are explained by habitat type rather than by rarity.

Aims: Inger *et al*. (2015. Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecol. Lett.* **18:** 28–36) concluded that in the period 1980–2009 populations of common European birds declined while less abundant species increased in number. The main aim of this paper is to test if this also holds for the Netherlands. Our first hypothesis proposes the opposite effect; namely that: (1) common birds have become more common and rare birds more rare. We tested three additional hypotheses: (2) that in the Netherlands, habitat type plays an important role in population change, with a strong decline of farmland species, (3) that larger birds have increased more than small birds; and (4) that insectivorous birds have decreased more than birds of other feeding guilds.

Methods: We used the same methodology as used by Inger *et al*. (2015) for 110 of the investigated 144 bird species that breed in the Netherlands.

Results: We found no significant effect on population change of rarity of the bird species in the Netherlands. So, neither the conclusion of Inger *et al*. (2015) nor our own contrasting hypothesis was supported. However, in line with our second hypothesis, we found a strong effect of habitat type, with a large decline of farmland species. In addition, we found an increase of forest and inland wetland species. These trends can mainly be attributed to agricultural intensification and a decrease in agricultural area, and to an increase of forest and inland wetland area and quality, respectively. Our third hypothesis was not supported. We found a non-significant positive effect of body weight on population trends. Finally, we found no support for our fourth hypothesis that insectivorous birds had declined.

Conclusions: We recommend further in-depth comparative analyses of bird trends in Europe, its regions and countries, as a basis for better-targeted conservation measures at different spatial scales.

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Introduction

Populations of many European birds have undergone major changes over the past decades. Understanding such trends is crucial for developing conservation strategies. However, major differences may occur between regional, national and European trends. Comparing such different trends can help to identify drivers, which in turn can guide conservation measures at various spatial scales.

In Europe strong negative trends have been reported for populations of farmland birds (Stoate *et al.* 2001, 2009, Donald *et al.* 2001, 2006, PECBMS 2008, Vorisek *et al.* 2010, Gregory *et al.* 2019, Bowler *et al.* 2019), which most authors attribute to agricultural intensification. Similar trends for farmland birds have been found at a country level in overlapping, though somewhat different, periods, for example, in England and Wales (Chamberlain *et al.* 2000), Sweden (Wretenberg *et al.* 2006), France (Jiguet *et al.* 2012), Hungary (Szép *et al.* 2012), Poland (Sanderson *et al.* 2013), Denmark (Bowler *et al.* 2019) and the Netherlands (Melman *et al.* 2008, 2016, Sovon Vogelonderzoek Nederland 2018).

Considering this general pattern, the analysis published by Inger *et al.* (2015) of European bird trends came as a surprise. They found that in the period 1980–2009 the rarity of species was a better predictor of population trends than other explanatory variables, such as habitat type, feeding guild and body weight. More specifically, common birds had, on average, become less common, while less abundant species had become more common.

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The authors focused on rarity, realising that in conservation policies insufficient priority had been given to more common species, despite their key role in ecosystem structure, function and services. This concern had previously been expressed by Gaston & Fuller (2008) and Vorisek *et al.* (2010). For the Netherlands, Van Turnhout *et al.* (2007) did not find a significant effect of rarity on population trends between 1973–1977 and 1998–2000, but a subsequent study, using a different definition of rarity, reported a significant negative effect of rarity on bird population trends in the Netherlands in the period 1990–2005 (Van Turnhout *et al.* 2010). In contrast, a Dutch study (Planbureau voor de Leefomgeving 2014) concluded that in the Netherlands, red-listed species of several plant and animal taxa combined had decreased over the period 1997–2010, whereas species that were not red-listed had increased over the same period. Although red-listed species do not fully coincide with rare species, this suggests that in the Netherlands common birds are becoming more common, while rare birds are becoming rarer. Planbureau voor de Leefomgeving (2014) attributed these trends to the ongoing homogenization of the landscape, leading to a strong decline of specific habitats. Earlier, Van Turnhout *et al.* (2007) had found increasing similarities between regional bird communities, which they attributed to landscape homogenization. However, none of these studies compared their results with the wider European trends, which is the main goal of the present study.

We systematically compared the trends in breeding bird abundance in the Netherlands with the European trends found by Inger *et al.* (2015), focusing on the same period (1980–2009) and using the same analytical methods. Our main hypothesis is that in the Netherlands, rarity can help explain the observed trends, but in the sense that common birds have become more common, while rare birds have become rarer – in contrast to the European trends.

As in the study by Inger *et al.* (2015), we investigated habitat type, body weight and feeding guild as additional explanatory variables. Recognizing patterns found in the literature (see above), we hypothesize habitat type to be the most important variable in the Netherlands, dominated by a decrease in farmland bird abundance. For body weight, we predicted an increase in populations of large birds in the Netherlands, given similar findings by Van Turnhout *et al.* (2010), and the clear increase in the field of several goose species, including Greylag Goose *Anser anser*, Mute Swan *Cygnus olor,* White Stork *Ciconia ciconia* and Common Buzzard *Buteo buteo* (Sovon Veldonderzoek Nederland 2018). At the European level, Inger *et al.* (2015) also found a general increasing trend (though not significant) for larger birds.

Unlike Inger *et al.* (2015), we also predicted differences in abundance trends dependent on feeding guild in the Netherlands, in particular a decrease in populations of insectivorous birds. This hypothesis was based on: (1) the decline of 12 insectivorous farmland bird species in the Netherlands in the period 2003–2009 (Hallmann *et al.* 2014), which was associated with concentrations of the neonicotinoid insecticide imidacloprid in surface waters, although Van Turnhout *et al.* (2010) did not find a significant decline of insectivores in the Netherlands between 1990 and 2005; (2) the decline of insectivorous birds in Europe between 1990 and 2015 (Donald *et al.* 2006, Bowler *et al.* 2019) and (3) the strong decline of insects found in nature protection areas in Germany between 1989 and 2016 (Hallmann *et al.* 2017, but see Van Klink *et al.* 2020 for a nuanced view) as well as the Netherlands between 1985 and 2017 (Hallmann *et al.* 2020). Here, we test our four hypotheses for the Netherlands and compare the results with the findings by Inger *et al.* (2015) at the European level.

Methods

General and nomenclature

To compare breeding bird population trends in Europe and the Netherlands, primarily focusing on the role of rarity as an explanatory variable, we used the same study period (1980–2009) and analytical methods as chosen by Inger *et al.* (2015). After compiling data on the abundance of breeding birds in the Netherlands, we investigated the trends in breeding bird abundance and the role of the different explanatory variables for the Netherlands, and whether these differed from those for Europe. Hereafter we briefly outline the different steps in the methodology, including all relevant steps by Inger *et al.* (2015). For some minor changes, aiming to reduce the complexity of the analysis by Inger *et al.* (2015), see online Appendix S1. Richard Inger kindly provided the data used for his analysis and his statistical program, adapted in such a way as to enable us to make the analyses as comparable as possible. We ensured that scientific names were standardized between the Dutch and the European data using Van den Berg (2019) and Gill & Donsker (2017) (Appendix S2).

Bird abundance estimates

We compiled abundance estimates of the Dutch breeding birds using two data sources: national abundance data for all species for a given year, and national trend indices of these species for each year (relative to these abundance data). Birdlife Europe kindly provided estimated abundance data for 236 bird species breeding in the Netherlands based on the third Dutch 'Atlas project' (Sovon Vogelonderzoek Nederland 2002), covering the period 1998–2000. We assume, as Inger *et al.* (2015) did, that the estimated number of breeding pairs in this period reflects the breeding population size in the year 2000. To estimate the abundance of each species, the geometric mean was taken of the minimum and maximum population estimates and this was multiplied by two. These estimates do not take into account the non-breeding population, and we assume, following Inger *et al.* (2015), that the number of breeding pairs also represents the size of the actual population. Sovon Vogelonderzoek Nederland kindly provided national trend indices for 183 breeding bird species in the Netherlands, based on the long-term Breeding bird Monitoring Project (BMP) (Sovon Vogelonderzoek Nederland 2019). These same trend indices were used in the Pan-European Common Bird Monitoring Scheme (PECBMS 2020), the source of the combined European trend indices used by Inger *et al.* (2015). These national trend indices were then applied to the national population estimates to produce abundance estimates for each species from 1980 to 2009. Of the 144 European breeding bird species included by Inger *et al.* (2015), 110 species also breed in the Netherlands (Appendix S2). For 101 of these 110 species, yearly trend data were available. For seven of these 101 species, records covered the whole period 1980–2009, while for 79 and 15 species yearly data were available from 1985 and 1990 respectively (the mean number of missing years at the start of the study period is 5.80, sd = 1.83). Population estimates for the missing years were extrapolated based on the abundances for the years for which indices were available. For each species with missing data, we first fitted four regressions (a linear regression or exponential regression, both using either the whole data set or only the first 10 years of available abundance data) to extrapolate the population size in the missing early years. We used the first Dutch Atlas project (1979) to check whether the resulting extrapolations (for 1980–1985 or 1980–1989) were realistic. We found that using data from the first 10 years resulted in more realistic estimates than using the whole data set for both linear and exponential regressions. Hence, for each species, we extrapolated missing data using the better-fitting regression (either linear or exponential) on the first 10 years of available data (Appendix S3). Yearly monitoring data were not available for nine species that breed irregularly in the Netherlands. For these species we used the abundance data from the four Dutch Atlas projects and linked these to the middle years of the four censuses (Teixeira 1979, Sovon Vogelonderzoek Nederland 1987, 2002, 2018). Trend indices for these nine species were then obtained by simple linear interpolation. In this way, complete national abundance data for the 110 Dutch species were compiled for the research period 1980–2009.

For the bird abundance per year for Europe, we used the European data (25 countries, 144 species) provided by Inger *et al.* (2015), abbreviated as EUR25. For a list of these 25 European countries, see Appendix S2. To compare the breeding bird trends in the Netherlands and in Europe, we created an European data set based on EUR25 excluding records from the Netherlands, and excluding all data for the 34 out of the 144 bird species studied by Inger *et al.* (2015) that do not breed in the Netherlands. This adapted European data set is abbreviated as EUR24. We then checked whether each adaptation of the European data set – corrections of body weights (explained later), subtraction of abundances of the Netherlands, and excluding the 34 non-Dutch breeding species – would have resulted in conclusions different to those reported in Inger *et al.* (2015). These analyses showed that only the exclusion of the 34 non-Dutch species from the European data set affected the European trends reported by Inger *et al.* (2015). While retaining the dominant role of the interaction between rarity (abundance quartile in Inger *et al.*, 2015) and time, the interaction between habitat types and time now also became important. Remarkably, however, the fraction of explained variance in the adapted European data set about halved. For full details see Appendix S4data set and the Discussion.

Finally, both data sets were adapted to reduce the noise associated with annual fluctuations, by smoothing the abundances using a generalized additive model with degrees of freedom 0.3 times the number of years in the data set (Fewster *et al.* 2000), as did Inger *et al.* (2015). In addition to the abundance estimates per species for both data sets, we also calculated biomass estimates using body weight data (body mass in Inger *et al.* 2015; the mean of male and female weights). We used the body weight data set provided by Inger, with corrections for 24 out of the 144 species using Dunning (2007) (Appendix S5). Biomass was calculated on the basis of the smoothed abundance data. So, for the analyses conducted to test the hypotheses, the following two data sets of 110 species were used: one for the Netherlands, and one for the Netherlands and Europe combined (EUR24).

Variables explaining species population trajectories

To assess differences in trends between common and less common species, all species were assigned to one of four quartiles based on their rarity (abundance quartile in Inger *et al.* 2015), with the least common species in quartile 1 and the most common in quartile 4 (termed here: Q1, Q2, Q3 and Q4). In line with Inger *et al.* (2015), we used the so-called 'variable quartiles' for the analyses. Variable quartile assignment was performed on a yearly basis allowing species to move between quartiles as their abundance changed, hence the species composition of the quartiles may change from year to year.

Three other species characteristics that may affect population trajectories were taken from Inger *et al.* (2015): habitat type (categorized as farmland, forest, inland wetland [inland water in Inger *et al.* 2015] and 'other habitat types' [other habitat, in Inger *et al.* 2015]), body weight, and main feeding guild (aerial insectivore, carnivore, granivore, herbivore, insectivore, and omnivore). We used the same habitat type and feeding guild classifications as Inger *et al.* (2015). Habitat type was taken by them from the PECBMS: farmland ($n = 25$ species), forest ($n = 25$), inland wetland ($n = 8$) and 'other habitat types' ($n = 52$). Feeding guild was based by them on feeding preferences used for most of the year, not including seasonal variation (taken from Snow & Perrins 1998, Handbook of the Birds of the World Alive 2013): aerial insectivore ($n = 7$), carnivore ($n = 5$), granivore ($n = 22$), herbivore ($n = 4$), insectivore ($n = 59$) and omnivore ($n = 13$).

Statistical analysis

All analyses were performed in R version 3.5.0 (R Core Team 2017). For all these analyses, we followed relevant parts of the approach described in detail by Inger *et al.* (2015), see Appendix S1 for excluded parts and minor differences in approach.

First, for both the Netherlands and Europe (EUR24), we assessed the temporal changes in the total abundance (the summed raw data of breeding bird abundances for all species) and total biomass (the sum of the products of species' abundances and body weights for all species). These were referred to as abundance and biomass, respectively, in Inger *et al.* (2015). We then focused our main analysis on two topics: (i) assessing the trends of breeding birds in the Netherlands (Netherlands data set), and (ii) assessing whether the relevant explanatory variables differed between Europe and the Netherlands (combined data set). The basis of the statistical analyses – to investigate the role of different variables in explaining the population trends – was a generalized linear mixed effects model with a Gaussian error structure, using the package 'lme4' (Bates *et al.* 2015).

Abundance was the response variable, with one record per species ($n = 110$) per year ($n = 30$). To minimize correlation between absolute abundances and rarity quartiles, species' abundances were z-transformed using species-specific means and standard deviations. Fixed factors included in the overall models were time (year, continuous integer variable), rarity (four-level categorical variable), feeding guild (six-level categorical variable), habitat type (four-level categorical variable), and body weight (continuous variable), as well as the interactions between time and each other variable. All fixed effects were also standardized using the 'arm' package (Gelman *et al.* 2018) to increase the interpretability of the parameter estimates (Schielzeth 2010). The interactions describe which changes occur over time related to these variables. Species was included in the model as a random factor: a random slope (by time) and intercept.

To evaluate the variance explained, the R^2 values of the model containing all the explanatory variables of interest were calculated using the methods of Nakagawa & Schielzeth (2013); where GLMM(m) represents the marginal R^2: variance explained by the fixed factors, and GLMM(c) the conditional R^2: variance explained by both fixed and random factors.

Model simplification and selection were performed using a multi-model inference approach based on the methods and recommendations of Burnham & Anderson (2002) and Grueber *et al.* (2011). The function 'dredge' in the package 'MuMIn' (Barton 2018) was used to produce all hierarchical subsets of the overall model and rank them based on Akaike information criterion corrected for small samples sizes (AICc). Following Richards (2008), all models with delta AICc < 2 were retained (referred to below as selected models). Model averaging was used to produce the averaged parameter estimates of the selected models and relative importance (RI) of each variable (Burnham & Anderson 2002). To determine the number of bird species demonstrating significant population declines or increases between abundance quartiles, we used linear regression models (response: abundance against year: explanatory fixed variable) for each species individually. Generalized additive models used to illustrate the trends on plots were carried out using the 'gam' package (Hastie 2018). To determine denominator degrees of freedom, F and *P* values were calculated using Satterthwaite (1946) approximations in package ‘lmerTest’ (Kuznetsova *et al.* 2017).

For the comparison between the regions of Europe (without the Netherlands) and the Netherlands (analysis ii), the three-way interaction between region, time and the key explanatory variables of interest were also included in the overall model described above. The ‘effects’ package of Fox & Weisberg (2018) was used to assess differences in slopes between regions. For most species, the first five years in the 30 year data series (1980–2009) contained extrapolated data, which may have affected the trends found. Therefore, we also analysed the shorter 25-year series (1985–2009), which resulted in similar trends (sign and size, data not shown). As we were interested in the comparison with Inger *et al.* (2015), here we report on the trends over the same period of 30 years.

Results

Trends in the Netherlands

Total abundance and total biomass

The total abundance of all 110 Dutch breeding birds showed a difference of 2.3 million birds between 1980 (20.3 million) and 2009 (22.7 million), which is a non-significant increase of 11.4% (Table 1 and Figure 1(a)). By contrast, the total biomass of all birds together showed a significant decrease of about 281 tonnes, or 9.5%, (Table 1 and Figure 1(b)). The trends for Europe (EUR24) in total abundance and total biomass are, despite the adaptations, very similar to those in EUR25 described by Inger *et al.* (2015) (Figure 1).

Abundance of individual species – explained variance

Standardized abundances of 110 bird species breeding in the Netherlands were used to determine the relevant explanatory variables explaining the trends. Below, we first describe the general model performance and results, and then present results in relation to the different explanatory variables and hypotheses: rarity, habitat type, body weight and feeding guild. See Appendix S6 for individual species abundance plots.

In our study, the overall regression model based on the data explained 51.4% of the variance in the breeding bird abundance, and 9.5% was explained by the fixed variables and their interactions (for R^2 see Appendix S5). There were eight selected models (Appendix S5) derived from the overall regression model. These models were used to produce averaged explanatory variable estimates (to be treated in the following section). The two-way interactions between the explanatory variables and time indicate how the abundances of the different species have changed over time in relation to these explanatory variables.

From the selected models we determined which explanatory variables were most important (Appendix S5) for the Netherlands. The interaction of habitat type with time was retained in six of the selected models with a Relative Importance (RI) of 0.799. Second best was the interaction of rarity quartiles with time, the crucial result in the Europe analysis of Inger *et al.* (2015); this interaction was retained in four of the selected models with an RI of 0.511. The interaction of body weight and time was retained in only two of the selected models, with an RI of 0.213. Finally, feeding guild and its interaction with time were not present in any of the selected models. We also ran a full model with all terms found in the individual selected models to get a picture of the overall significances of the different terms.

Rarity

Rarity clearly contained some explanatory power (as the term was maintained in interaction form in half of the candidate models). However, the interaction between rarity and time was not significant in the full model ($F = 1.955$, df = 3, 112, $P = 0.119$). The regression coefficients (β) ± standard errors (se) for the different quartiles are: Q1: 0.316 ± 0.391; Q2: 0.353 ± 0.390; Q3: 0.162 ± 0.388; Q4: 0.109 ± 0.409.

Habitat type

For the best explanatory variable, habitat type, we present, in addition to the results of the statistical analyses, also some visualizations of these results. In the full model the interaction between habitat type and time was significant ($F = 5.039$, df = 3, 1522, $P = 0.003$). Farmland birds showed a negative trend over time ($\beta \pm \text{SE} = -0.638 \pm 0.405$). By contrast, we found an increasing trend ($\beta \pm \text{se}$) for forest: 0.588 ± 0.355, for inland wetland: 0.894 ± 0.582 and for ‘other habitat types’: 0.096 ± 0.235.

The changes in total abundance and total biomass related to the explanatory variable habitat type in the Netherlands are summarized in Table 1 and Figure 2. Most of these changes were related to farmland and ‘other habitat types’ (taken together, approximately 80% for total abundance and 90% for total biomass). For farmland, a strong decline of 40% was found in total abundance and a 45% decline in total biomass. For forest species, by contrast, both total abundance and total biomass showed a very strong increase of 88% and 75%, respectively. Inland wetland species also showed a strong increase in

Table 1. (a) Changes in total abundance and total biomass (in tonnes) of those 110 breeding birds selected for the comparison between the Netherlands and Europe (EUR24) in the period 1980–2009 per habitat type and, (b) number of species with changing abundance and the number for which these changes were statistically significant ($\alpha = 0.05$) per habitat type.

(a) Total abundance and total biomass

Habitat type	1980	2009	Change	Fraction of total change	Fraction of row change
Total abundance	20349152.5	22672777.4	2323624.9		0.114
Farmland	5136683.9	3025085.7	−2111598.2	0.323	−0.411
Forest	1276719.0	2408020.6	1131301.6	0.173	0.886
Inland wetland	500832.7	695947.4	195114.7	0.030	0.390
Other habitat types	13434916.9	16543723.7	3108806.8	0.475	0.231
Total biomass (tonnes)	2968.6	2687.0	−281.6		−0.095
Farmland	469.7	264.7	−205.3	0.568	−0.436
Forest	48.1	84.7	36.6	0.101	0.761
Inland wetland	7.3	10.3	3.0	0.008	0.411
Other habitat types	2443.5	2328.3	−116.2	0.322	−0.048

(b) Number of changing species

	No. species		No. species significantly	
	Increasing	Decreasing	Increasing	Decreasing
All species	58	52	51	43
Farmland	8	17	6	16
Forest	16	9	14	4
Inland wetland	7	1	6	1
Other habitat types	27	25	25	22

both total abundance (39%) and total biomass (41%). Species of 'other habitat types' showed an increase of 20% in total abundance, but the total biomass showed a small decrease of about 5%.

The largest number of shifts of individual species took place within the habitat types farmland (48%) and forest (44%) (Table 1). Of the 42 of the 110 species that did move between rarity quartiles in the research period, 10 species had, in the final year, returned to the starting quartile, 16 moved to a more abundant quartile (farmland: 3, forest: 5, inland water: 2, other: 6) and the remaining 16 moved to a less abundant quartile (farmland: 7, other: 7, forest: 2), see also Table 1.

Body weight

In the full model the interaction between body weight and time was not significant ($F = 2.435$, df = 1, 111, $P = 0.121$). The averaged explanatory parameter estimate for the trend in time for body weight was positive: $\beta \pm \text{se} = 0.463 \pm 0.280$; so larger birds had a non-significantly stronger increase in time than had smaller birds.

Feeding guild

Neither the main term, nor the interaction of feeding guild with time was present in the selected candidate models; so, based on these analyses feeding guild is not a significant explanatory variable. Given the recent reports of a steep decline in insect populations (see Introduction), we conducted a further analysis into feeding guild as an explanatory variable, focusing on insectivores. In this analysis we did not find a significant change in the abundance of the insectivores that was linked to habitat type (e.g. a decrease in farmland but not in inland wetland; three-way interaction of habitat type-feeding guild-time in the overall regression model: $F = 1.002$, df = 10, 108.5, $P = 0.435$). For the insectivores of Hallmann *et al.* (2014), we found a non-significant decline over time ($\beta = -0.0412$, df = 61.1, $P = 0.118$), whilst the remaining insectivore species showed a slightly positive, non-significant increase ($\beta = 0.0163 \pm 0.01229$, df = 61.1, $P = 0.189$). For full description of these additional analyses, see Appendix S8.

Trends in the Netherlands versus the rest of Europe

We checked whether the interactions of the most important explanatory variables of rarity and habitat type on the one hand, and time on the other hand, were significantly different between the 'regions' the Netherlands and Europe (without the Netherlands). We did not examine this for body weight and feeding guild, since for neither the Netherlands nor Europe did these appear to be important drivers of breeding bird abundance.

Rarity

The three-way interaction between region, rarity and time was significant ($F = 47.35$, df = 3, 6452, $P < 0.001$). Post-hoc tests showed that for three of the four rarity quartiles, the trends for the Netherlands differed from those for the rest of Europe. For the least common

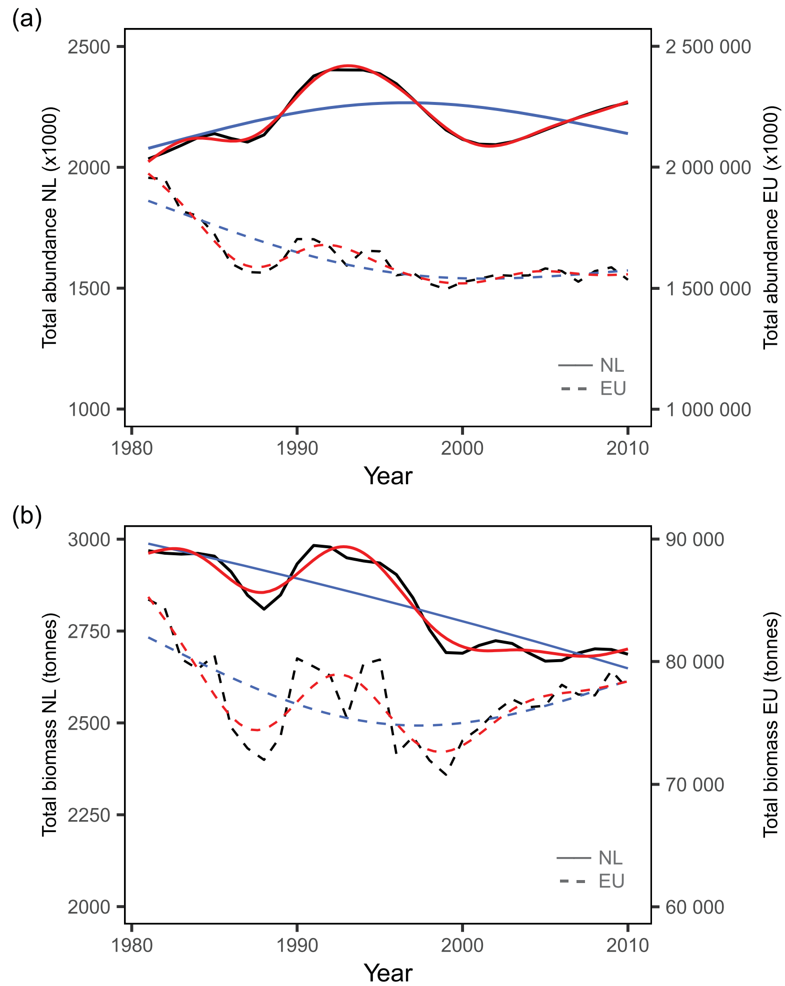

Figure 1. Changes in total abundance (above) and total biomass (below, in tonnes) of all selected 110 breeding birds in the Netherlands and in Europe (EUR24), left and right vertical axis respectively, in the period 1980–2009. Black lines represent the total abundance and total biomass estimates from 1980 to 2009; coloured lines represent the fitted values from a general additive model (red line: $k = 10$, blue line: $k = 3$). In the Netherlands, there was a c. 11% increase in total abundance in 2009 compared with 1980, but linear regression revealed no significant change of the total abundance over this period ($\beta = 21.046 \times 103$, $t = 0.876$, $P = 0.389$). However, there is a significant decrease of total biomass ($\beta = -11.70$, $t = -8.757$, $P < 0.0001$).

bird species (Q1), trends in the European and the Dutch data did not differ, while both showed a small (and not significantly different) increase (contrast = -0.0047 ± 0.0060, df = 6518, $t = -0.782$, $P = 0.434$). For the next quartile (Q2), again both regions showed an increase, however with a faster increase in the Netherlands (contrast = -0.0379 ± 0.0066, df = 6218, $t = -5.742$, $P < 0.001$). The third quartile (Q3) showed a small increase for the Dutch data as opposed to a small decline for the European data (contrast = -0.0398 ± 0.0066, df = 6234, $t = -6.032$, $P < 0.001$). The most common bird species quartile (Q4) showed a small increase for the Dutch data, but a strong decline for the European birds (contrast = -0.0682 ± 0.0066, df = 6508, $t = -10.540$, $P < 0.001$). In summary, in Europe rarer birds (Q1 and Q2) showed an increase, while more common birds showed a decline (cf. Inger *et al.* 2015); by contrast, in the Netherlands there was a non-significant increase for all rarity quartiles.

Habitat type

The three-way interaction between region, habitat type and time was significant ($F = 127.27$, df = 3, 6488, $P < 0.001$). Both the European and the Dutch data showed a strong decline for farmland species, which did not differ significantly between these two regions (contrast = -0.004 ± 0.005, df = 6433, $t = 1.85$, $P = 0.440$). However, trends differed significantly for the habitat types forest and inland wetland, where we found declines for Europe as opposed to increases for the Netherlands (forest contrast = -0.050 ± 0.006, df = 6453, $t = -8.57$, $P = 0.44$; inland water contrast = -0.103 ± 0.010, df = 6416, $P < 0.001$). For ‘other habitat types’ both regions showed a modest increase, though somewhat (not significantly)

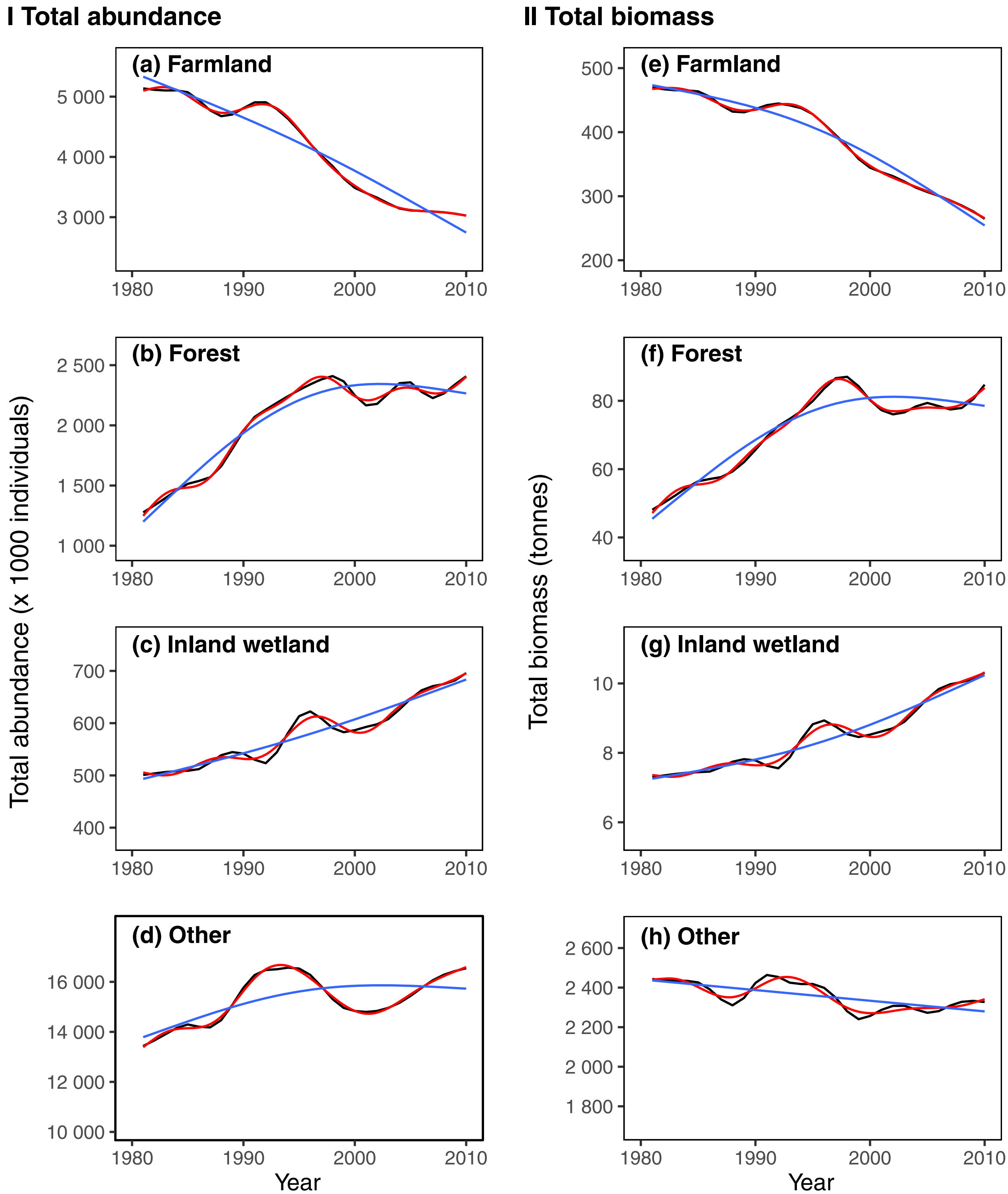

Figure 2. Total abundance and total biomass (tonnes) of breeding birds per habitat type in the Netherlands. Left figures (a–d): total abundance, right figures (e–h): total biomass. Black lines represent the total abundance and total biomass estimates from 1980 to 2009; coloured lines represent the fitted values from a general additive model (red line: $k = 10$, blue line: $k = 3$); Other = 'other habitat types'.

bigger for Europe (contrast=0.0074, df = 6413, $t = 1.851$, $P = 0.0642$). So, while in the original analysis by Inger *et al.* (2015) habitat type did not significantly affect the trend over time, this trend was significant in the adapted European data set (EUR24) and showed similar trends to the Netherlands for the habitat types 'farmland' and 'other habitat types' and contrasting trends to the Netherlands for forest and inland wetland.

Discussion

Total abundance and total biomass

Breeding birds in Europe have shown a considerable decline over recent decades. Inger *et al.* (2015) found a 20% decline in the total abundance and a more moderate 7% decline in their total biomass. In contrast to Inger *et al.* (2015), we found an 11% *increase* (though not significant) in total abundance for the Netherlands, but a comparable 9.5% decline in total biomass. Van Strien *et al.* (2016) also found a modest increase in abundance in the period 1990–2014, and Vorisek *et al.* (2010) also found a 13% decline in total biomass of common birds in 21 European countries in the period 1980–2006.

Abundance of individual species

The overall regression model used in our study for the Netherlands explained 51% of the variance in the data and the fixed explanatory variables explained 9.5%. In the study by Inger *et al.* (2015) for Europe (EUR25) the corresponding conditional and marginal results were considerably higher: 76% and 38%, respectively. However, for Europe without the Netherlands (EUR24) the overall regression model explained much less of the variance explained by Inger *et al.* (2015) for EUR25: 40% and 15%, respectively – more similar to our results. This strong drop in explained variance when those European birds that do not breed in the Netherlands are excluded may be due to either stronger abundance trends of these excluded species, or much lower variance around their abundance estimates, compared with the Dutch breeding species. Since these excluded species are mainly southern species, we speculate that biogeographical factors in the southern climate lead to lower population fluctuations over time, compared with the temperate and boreal climates. Moreover, methodological differences between countries (for example, survey plot size, which is relatively small in the Netherlands) may also result in differences in noise around abundance estimates.

Rarity

We found a significant difference between the trends per rarity quartile for the Netherlands and those for Europe (EUR24), neither in line with Inger *et al.* (2015) nor with our own hypothesis. For the Netherlands, we expected a decrease of rarer species and an increase of commoner species. In partial contrast, we found a non-significant increase in all quartiles for the Netherlands. The largest difference with Inger *et al.* (2015) concerned the most common species: in Inger's study this group showed a strong decline, whereas in the Netherlands the species in this quartile showed a (non-significant) increase, although lower than the species in other quartiles. For the rare species both Inger *et al.* (2015) and our study showed an increase. Here we should keep in mind that, except for small, isolated populations, rarity is not, by itself, a causal factor for influencing bird trends. Rather it is a result of other factors playing a role. First, there is the role of homogenization of the landscape, which facilitates – often already common – species of common habitats to become even more common (Planbureau voor de Leefomgeving 2014). Further, we observe in the Netherlands an increasing interest in the conservation of common birds, as reflected by, for instance, urban censuses and the encouragement of bird-friendly gardens.

Rather than an increase of moderately common species, Van Turnhout *et al.* (2007) found a decline of both very rare and very common species in the Netherlands in the period 1973–1977 to 1998–2000, but neither of these trends was significant. In a later study that covered the overlapping period 1990–2005, Van Turnhout *et al.* (2010) assessed abundance trends of 170 breeding birds in the Netherlands, using three different rarity metrics: Dutch population size, Dutch range size and European range size. In their multivariate models, they found no significant relationship between bird abundance trends and population or range size at the national level. However, in these models the rarity metric of the European range size showed a significant negative relation with bird abundance: birds with smaller range sizes (generally the relatively rare species, such as the Little Egret *Egretta garzetta*) showed stronger increases than those with larger range sizes (the relatively common species). Unlike in our study, no allowance was made for differential or non-linear trends in abundance over time along a rarity gradient, e.g. decrease at extreme abundances (very rare and very common), whilst increases at intermediate abundances.

Habitat type

Habitat type appeared to be the strongest explanatory variable in the Netherlands. For this factor, our hypothesis was supported. This effect was dominated by the decrease of farmland birds, presumably largely due to agricultural intensification and to a lesser extent to a decrease of farmland area of about 8% over the study period (CBS 2019). In contrast, we found a significant increase of breeding birds in forests and in inland wetlands. For forest birds, this may be explained by a concomitant 17% increase in forested area (from 2940 km^2 in 1979 to 3454 km^2 in 2010, CBS *et al.* 2016a), a partial shift from pine forests to typically more species-rich deciduous forests, and changed forest management, which has resulted in an increased average forest age and more decaying trunks on the forest floor. The increase in inland wetland birds may be explained by a 61% increase of inland wetland area (from 209 km^2 in 1990 to 338 km^2 in 2012, CBS *et al.* 2018), improved water quality and inland wetland management (CBS *et al.* 2016b). Our directions of the trends in forests, farmland and wetland birds are in line with Van Turnhout *et al.* (2007) and Gregory *et al.* (2019), who reported no major changes in forest birds, but a steep decline in farmland birds. By contrast, Inger *et al.* (2015) found no significant effect of habitat type at the European level. This finding remains surprising, also in view of the Europe-wide intensification and mechanization of agriculture. However, this development has not occurred to the same extent and at the same speed across the whole of Europe. In Central and Eastern Europe even extensification and land abandonment took place after 1989 (Donald *et al.* 2001, Stoate *et al.* 2009, Vorisek *et al.* 2010, Reif *et al.* 2008 [on the Czech Republic], Baldí & Batáry 2011 [on Hungary] and Sanderson *et al.* 2013 [on Poland]). In Sweden intensification took place at the same time as did land abandonment and afforestation (Wretenberg *et al.* 2006). These contrasting patterns of development may well have weakened habitat type as an explanatory factor when all regions are combined. This conjecture is supported by our finding that habitat type became an important explanatory variable at the European level once we focused on those 110 species breeding in the Netherlands.

Body weight

We found a positive correlation between body weight and population size trends over time, as we had expected, but this was not significant. This factor did not significantly contribute to the explanation of the bird trends for the Netherlands or for Europe (EUR24) in this study, nor did it in the study of Inger *et al* (2015, EUR25). In their multivariate models, Van Turnhout *et al.* (2010) found that the relationship between male body weight and rarity was dependent on the chosen rarity metric: the smaller the European range size – one of the metrics – the larger the effect of body weight on abundance trends. Larger birds, particularly rare larger birds, showed a stronger increase in abundance.

One possible explanation for our lack of an effect of body weight is the exclusion of goose species in this study, as mentioned earlier, following Inger *et al.* (2015). As geese are among the heaviest breeding birds, and goose abundance has increased strongly in the Netherlands during the study period (Sovon 2018), omitting this species group will have contributed to the weaker effect of body weight than noted by Van Turnhout *et al.* (2010). This also helps to explain why, as noted, we found a decline in total biomass, as opposed to an increase in total abundance.

Feeding guild

We did not find significant differences in the abundance trends between feeding guilds in our study, despite strong declines of flying insects found in nature protection areas in Germany (Hallmann *et al.* 2017), of macro-moths, beetles and caddisflies in The Netherlands (Hallmann *et al.* 2020), and of insectivorous birds in the Netherlands (Hallmann *et al.* 2014) and elsewhere in Europe (Bowler *et al.* 2019). Donald *et al.* (2006) reported a decline of every feeding guild in Europe in the period 1990–2000, but only significantly so for insectivores. By contrast, Van Turnhout *et al.* (2010) found an *increase* in all feeding guilds in the Netherlands in 1990–2005, though only significant for herbivores. The classification and definition of indicators is known to strongly affect bird trends (Gregory *et al.* 2019). Indeed, the definition of 'insectivorous birds' may well be relevant here. For instance, Inger *et al.* (2015) categorized Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* as insectivorous species and the Grey Heron *Ardea cinerea* as a carnivore; classifications which could be disputed. Further analyses may, for instance, be based on the Elton traits 1.0 index (Wilman *et al.* 2014), as used by Bowler *et al.* (2019) in their comparison of Danish and wider European trends.

Regression to the mean

A methodological point that might be relevant for the interpretation of the observed trends concerns the aspect of data gathering. This not only applies to the selection of investigated species but may also be relevant for the choice of the statistical methods used. Particularly relevant here is the phenomenon called 'regression to the mean' (RTM) (Barnett *et al.* 2004, Kelly & Price 2005). This implies that in consecutive measurements within measurement series, high values of a random variable will generally be followed by lower values, and lower values by higher values. This phenomenon is of particular importance in data with considerable measurement errors (Kelly & Price 2005), such as those derived from visual and auditory observations of birds. All else being equal, when estimating bird abundance, a subgroup with a mean lower than the group average will have a higher mean at the next measurement, while the subgroup with a mean higher than the group average will tend to decrease (Barnett *et al*. 2004, Kelly & Price 2005). The main European result of Inger *et al.* (2015), that common bird species are declining rapidly while numbers of rare species are rising, follows the patterns expected by the statistical phenomenon of RTM, while the Dutch national trends do not show patterns consistent with this phenomenon.

Recommendations

Our study arrives at four recommendations for further research. First, we recommend that further trend studies be carried out at the national or regional level in order to obtain a better understanding of the relevant explanatory variables at different spatial scales. Second, we suggest that further analyses of trends should include statistical approaches that fully account for statistical phenomena such as RTM. Third, we recommend that future studies should include *all* regularly breeding bird species in the analyses. Fourth, we suggest that future studies should take other, or more detailed, explanatory variables into account. Van Turnhout *et al.* (2010) included 25 life-history, behavioural and ecological traits in their study of bird trends in the Netherlands. However, they did not use habitat type, which explained most variance in our study. Further study may include additional and more differentiated habitat types than we did, as well as landscape heterogeneity. Feeding guilds may also be more differentiated, as discussed for insectivores. Distinctions may also be made between specialists and generalists in several respects (e.g. Julliard *et al.* 2004, Wretenberg *et al.* 2006), between species groups with different nesting locations (Van Turnhout *et al.* 2010) and with different migratory strategies (Sanderson *et al.* 2006, Møller 2008, Vorisek *et al.* 2010, Van Turnhout *et al.* 2010, Szép *et al.* 2012, Gregory *et al.* 2019, Bowler *et al.* 2019), between native and introduced species, and between species listed and not listed in Annex 1 of the EU Birds Directive (Donald *et al.* 2007).

While European conservation laws, such as the Birds Directive, are an important and effective priority-setting policy tool (well documented by Donald *et al.* 2007), many conservation measures are implemented at the national level, where trends and their driving factors may well be different. An in-depth understanding of these trends and factors will allow customized and more effective conservation strategies, and ultimately improve bird conservation at the regional as well as the European level.

We end with three recommendations regarding conservation practice for the Netherlands: (i) to continue the successful management of forests and wetlands, (ii) to intensify efforts to include the conservation of biodiversity into sustainable farming practices and policies, and (iii) to broaden conservation strategies from the present focus on rare birds to also include the more common species.

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