

Continent-scale global change attribution in European birds - combining annual and decadal time scales

PETER SØGAARD JØRGENSEN¹, KATRIN BÖHNING-GAESE^{2,3}, KASPER THORUP⁴, ANDERS P. TØTTRUP⁴, PRZEMYSŁAW CHYLARECKI⁵, FRÉDÉRIC JIGUET⁶, ALEKSI LEHIKOINEN⁷, DAVID G. NOBLE⁸, JIRI REIF⁹, HANS SCHMID¹⁰, CHRIS VAN TURNHOUT^{11,12}, IAN J. BURFIELD¹³, RUUD FOPPEN^{12,14,15}, PETR VOŘÍŠEK^{9,16}, ARCO VAN STRIEN¹⁷, RICHARD D. GREGORY¹⁸ and CARSTEN RAHBEK⁴

¹Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark, ²Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt (Main), Germany, ³Department of Biological Sciences, Goethe Universität, Max-von-Laue-Straße 9, 60438 Frankfurt (Main), Germany, ⁴Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark, ⁵Museum & Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland, ⁶UMR7204 MNHN-CNRS-UPMC, CRBPO CP51, 55 Rue Buffon, 75005 Paris, France, ⁷Zoological Unit, Finnish Museum of Natural History, University of Helsinki, P. O. Box 17 FI-00014 Helsinki, Finland, ⁸British Trust for Ornithology, The Nunnery, Thetford Norfolk IP24 2PU, UK, ⁹Department of Zoology and Laboratory of Ornithology, Faculty of Science, Palacký University Olomouc, 17. listopadu 50, 771 43 Olomouc, Czech Republic, ¹⁰Swiss Ornithological Institute, Seerose 1, CH-6204 Sempach, Switzerland, ¹¹Sovon Dutch Centre for Field Ornithology, P.O. Box 6521 6503 GA Nijmegen, The Netherlands, ¹²Department of Animal Ecology, Institute for Wetland and Water Research, Radboud University Nijmegen, Toernooiveld 1, 6500 GL Nijmegen, The Netherlands, ¹³BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, UK, ¹⁴Dutch Centre for Field Ornithology, P.O. Box 6521 6503 GA Nijmegen, The Netherlands, ¹⁵European Bird Census Council (EBCC), P.O. Box 6521 6503 GA Nijmegen, The Netherlands, ¹⁶Pan-European Common Bird Monitoring Scheme, Czech Society for Ornithology, Na Bělidle 252/34, CZ-150 00 Prague 5, Czech Republic, ¹⁷Statistics Netherlands, Post Office Box 24500, The Hague 2490 HA, The Netherlands, ¹⁸Royal Society for the Protection of Birds, The Lodge, Sandy SG19 2DL, UK

Abstract

Species attributes are commonly used to infer impacts of environmental change on multiyear species trends, e.g. decadal changes in population size. However, by themselves attributes are of limited value in global change attribution since they do not measure the changing environment. A broader foundation for attributing species responses to global change may be achieved by complementing an attributes-based approach by one estimating the relationship between repeated measures of organismal and environmental changes over short time scales. To assess the benefit of this multiscale perspective, we investigate the recent impact of multiple environmental changes on European farmland birds, here focusing on climate change and land use change. We analyze more than 800 time series from 18 countries spanning the past two decades. Analysis of long-term population growth rates documents simultaneous responses that can be attributed to both climate change and land-use change, including long-term increases in populations of hot-dwelling species and declines in long-distance migrants and farmland specialists. In contrast, analysis of annual growth rates yield novel insights into the potential mechanisms driving long-term climate induced change. In particular, we find that birds are affected by winter, spring, and summer conditions depending on the distinct breeding phenology that corresponds to their migratory strategy. Birds in general benefit from higher temperatures or higher primary productivity early on or in the peak of the breeding season with the largest effect sizes observed in cooler parts of species' climatic ranges. Our results document the potential of combining time scales and integrating both species attributes and environmental variables for global change attribution. We suggest such an approach will be of general use when high-resolution time series are available in large-scale biodiversity surveys.

Keywords: citizen science, climate change, farmland birds, global change attribution, land-use change, multiple temporal scales, multiscale inference, population time series

Received 7 August 2014; revised version received 22 June 2015 and accepted 9 August 2015

Correspondence: Peter Sogaard Jørgensen, Global Economic Dynamics and the Biosphere, Royal Swedish Academy of Sciences, Box 50005, SE-104 05 Stockholm, Sweden, tel. +4560249579, fax +46-(0)8-152464, e-mail: psjorgensen@kva.se

Introduction

Lack of knowledge about the causes of long-term biological change (Araújo *et al.*, 2005; Araujo & Rahbek, 2006; Brown *et al.*, 2011; Parmesan *et al.*, 2011, 2013) is a potential factor limiting the reliability of ecological forecasts (Clark *et al.*, 2001) and indicators (Niemi & McDonald, 2004). Consequently, improved attribution to changing environmental conditions has repeatedly been called for in order to more reliably predict the future state of biodiversity (Araujo & Rahbek, 2006; Araujo & Townsend Peterson, 2012; Parmesan *et al.*, 2013) and to promote decision making based on accurate interpretation of the past and present (Parmesan *et al.*, 2011, 2013). Such improvements might be particularly urgent in large-scale monitoring schemes (Clark *et al.*, 2001; Scholes *et al.*, 2008; Parmesan *et al.*, 2013), which often provide the basis for forecasts (e.g. Huntley *et al.*, 2008; Araújo *et al.*, 2011) as well as indicators (e.g. Gregory *et al.*, 2005; Collen *et al.*, 2009; Butchart *et al.*, 2010).

One strategy toward a broader foundation for global change attribution is to complement inference of long-term change explained by organismal attributes and environmental conditions (e.g. Parmesan & Yohe, 2003; Fig. 1b) with inference over shorter time scales using

repeated observations of short-term population and environmental changes (Fig. 1c, Parmesan, 2006; Parmesan *et al.*, 2013). Each approach has its own strengths and weaknesses. In particular, long-term responses are often more readily available than e.g. annual resolution data. Secondly, global change hypotheses can efficiently be tested using simple relations with often readily available attribute or environmental data (Fig. 1b). Finally, long-term changes also occur at the same temporal extent as the investigated global changes, time scales which may be less prone to environmental and demographic stochasticity. On the other hand, investigators run the risk of overfitting long-term responses and concluding from spurious correlations in cases with several hypothesized driving environmental variables. In contrast, a more desirable statistical (e.g. Cormont *et al.*, 2011) and interpretative functional framework (e.g. LaDeau *et al.*, 2007; Parmesan *et al.*, 2013) is provided by focusing on changes over shorter temporal extents at which species reproduce (Fig. 1c). In particular, repeated measurement of the association between short-term demographic and environmental change allows to more robustly assess the relative evidence for and uncertainty of environmental drivers.

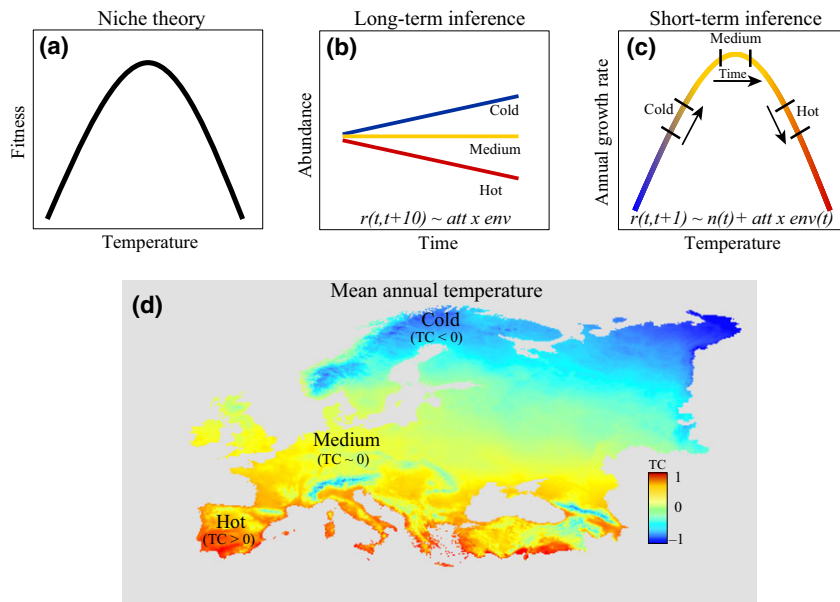


Fig. 1 Multiscale attribution of population size change to continental environmental change, exemplified with temperature increase. Functional relationships between species performance and one or more environmental variables (a) are often used to explain long-term differences in growth rates between populations located in different geographical environments (b), e.g. thermal environments (d). By characterizing the statistical relationship between annual growth rates ($r(t, t + 1)$) and changing environmental conditions ($env(t)$), short-term inference (c) can complement and validate long-term inference (b) based on decadal growth rates ($r(t, t + 10)$), organismal attributes (att) and environmental states (env). This combined analysis of multiple temporal scales broadens the basis for global change attribution. Thermal coordinate (TC) ranges from -1 to 1 and is illustrated for a hypothetical species distributed across Europe (d). Black arrows in (c) indicate the expected change in annual growth rates over time as temperature increases. In (b), abundance is standardized to a common initial value.

With their near continental coverage, the long running annual European surveys of breeding bird abundance provide a rare opportunity to apply this multiscale approach to global change attribution at a large spatial scale (Crick, 2004; Gregory *et al.*, 2005; Parmesan *et al.*, 2011). Yet even in these surveys, as well as in the North American counterpart (Sauer & Link, 2011), assessment of environmental change effects from shorter time scales is still much less common than analysis of long-term responses using organismal attributes (Table S1). For example, the effect of weather conditions on annual population growth rates was only recently investigated at national and regional scales (Table S1, e.g. Albright *et al.*, 2011; Cormont *et al.*, 2011). There is thus still a need to assess the benefit of combined long and short-term inference at a continental scale, including the ability to untangle responses to multiple global changes, such as climate and land use change (Parmesan *et al.*, 2013).

Marked changes in the European community of breeding birds have given rise to several hypotheses about the impact of climate and land use change (e.g. BirdLife International, 2004). Over the past decades long-distance migrants and farmland specialists have declined (Donald *et al.*, 2001, 2006; Sanderson *et al.*, 2006; Jiguet *et al.*, 2010a) in comparison to permanent residents, short-distance migrants (Gregory *et al.*, 2007; Van Turnhout *et al.*, 2010) and habitat generalists (Davey *et al.*, 2011). In addition, populations of hot-dwelling species, i.e. species in the local community with geographical ranges centered in warmer climates, have increased in abundance (Gregory *et al.*, 2009; Jiguet *et al.*, 2010a,b). Although climate and land use change are thought to be major underlying causes of these trends (BirdLife International, 2004; Crick, 2004; Green *et al.*, 2008; Gregory *et al.*, 2009), much remains to be learnt about the observed changes and their drivers (e.g. Knudsen *et al.*, 2011).

A basic but important step in any analysis of environmental effects is to settle on a relevant and manageable set of candidate environmental variables to investigate. For European birds, a combination of prior findings and theoretical considerations provide a good starting point for this identification. For example, two main processes have been proposed to explain the impact of climate change on birds with different migratory strategies. First, limited phenological response of long-distance migrants to earlier spring events associated with spring greening can lead to a mismatch with the peak of food resource availability (Both *et al.*, 2006, 2010). In comparison to long-distance migrants, short-distance migrants adjust faster to an earlier onset of spring and are consequently thought to benefit in terms of increased population size (Crick, 2004; Thorup *et al.*,

2007). A second process acts through increased survival and recruitment of resident birds in response to warmer winters (Hilden, 1989; Saether *et al.*, 2000; Gregory *et al.*, 2007). In turn, warmer winters can lead to a scarcity of e.g. nesting resources when migrants arrive at the breeding grounds (Ahola *et al.*, 2007; Lemoine *et al.*, 2007). Other suggested drivers of declines in long-distance migrants relate to drought conditions in the Sub-Saharan wintering areas (Baillie & Peach, 1992; Vickery *et al.*, 2013) and the relative importance of these changes in climate in the breeding and wintering areas of long-distance migrants remains poorly understood (Jones & Cresswell, 2010; Knudsen *et al.*, 2011; Vickery *et al.*, 2013). From a more theoretical standpoint, climatic conditions during the breeding season and the period of early juvenile survival are likely to influence recruitment into the breeding population in species with offspring starting to breed the subsequent year (Lande *et al.*, 2003), such as many common terrestrial breeding birds. The relative importance of these bioclimatic factors has, however, rarely been investigated across a larger number of species. Instead, many global change hypotheses originate from investigation of a single factor across many species or analysis of a single species' response to multiple factors. This lack of knowledge increases the uncertainty about the generality of suggested climate change impacts (e.g. Knudsen *et al.*, 2011).

Whereas the impact of climate change is usually attributed to a confined set of factors, avian land use change impacts in general involves a wider range of drivers (BirdLife International, 2004); chief among them in temperate regions is agricultural intensification (Newton, 1998). In recent decades, agricultural intensification has led to large declines in European farmland birds (Donald *et al.*, 2006; Voříšek *et al.*, 2010). Contributing to these declines is a lower availability of farmland nesting habitat caused by increased soil tillage, and a loss of noncrop matrix habitat (Benton *et al.*, 2002; Newton, 2004). At the local scale, the fecundity and survival of farmland specialists can be negatively affected by a lack of insect food resources, for example caused by the increased use of pesticides (Benton *et al.*, 2002; Boatman *et al.*, 2004). Due to this complex set of changes, investigations of land use change impacts at larger spatial scales often have to use surrogate environmental variables for agricultural intensification, such as crop yield (e.g. Donald *et al.*, 2001).

In the present study, we investigate the benefit of a combined attribution approach in linking recent major changes in the European breeding bird community to proposed driving climate and land-use change variables, using common farmland birds as the specific case. We compare evidence for a range of global change

hypotheses at two time scales using two complementary approaches, one relying mainly on organismal attributes as explanatory variables (long-term time scale) and one combining attributes with temporally varying environmental variables (short-term time scale). Specifically, we seek to address the following questions: (1) to what degree do inferences at each time scale support and complement each other with regard to impacts of land use and climate change? (2) Do effects of changing weather conditions correspond with expectations that winter warming and advancing spring will benefit early breeding species and be detrimental to late breeding species? (3) What is the relative importance of environmental change to the breeding or the wintering grounds for populations of highly mobile species such as long-distance migrants? (4) Does analysis of short-term population changes provide new insight to the types of climate change that may be causing poleward shifts in species abundance? Finally with regard to land-use change, (5) are farmland specialists particularly vulnerable to agricultural intensification?

Materials and methods

Study approach

We analyzed log-scale population growth rates estimated from time series of national count estimates of 51 common European breeding birds that all use farmland as a breeding habitat. The investigated species including passerines (Passeriformes), pigeons (Columbiformes), woodpeckers (Piciformes; Table S2) are in Europe characterized by having offspring born in an undeveloped state requiring feeding by adults (altricial offspring), and by offspring recruitment into the breeding population in the subsequent year (Cramp *et al.*, 1994). Applying a model selection approach to the analysis of 820 populations, we first looked at long-term population growth rates in relation to species and population-level attributes, thereby seeking to identify major changes over the past two decades associated with functional characteristics (Fig. 1b). Then, by combining attributes and temporally varying environmental variables, we compared annual scale support for global change hypotheses rooted in the findings from analysis of long-term growth rates (Fig. 1c). In the long-term analysis we also included means of environmental variables when their variation at the annual scale was likely to be driven by a diversity of natural and human factors (Fig. 1b, see long-term model). We do not try to relate long-term environmental changes to long-term population growth rates because an in-depth analysis of the existing set of hypotheses would result in a low sample size to predictor variable ratio. This low ratio arises for two reasons. (1) The number of functional traits required to capture the functional diversity of the investigated species combined with the number of environmental variables required to capture the diversity of environmental changes hypothesized to drive species changes. (2) The number of met-

rics required to capture the diversity of ways in which long-term environmental change may result in a long-term species response (e.g. through linear change, long-term or short-term extremes, increased variability etc.).

Time series came from a European data set coordinated by the Pan-European Common Bird Monitoring Scheme (PECBMS), led by the European Bird Census Council (EBCC), BirdLife International and Royal Society for the Protection of Birds (Gregory *et al.*, 2005). In this collaborative initiative, a large number of annual counts conducted by skilled volunteers are summarized to produce annual countrywide count estimates that are converted into population indices (PopIndex, index at $t_0 = 100$) with associated error estimates. Population indices and growth rates are calculated using the TRIM software, which applies Poisson regression while accounting for missing observations through imputation methods (for further details, see: Ter Braak *et al.*, 1994; Pannekoek & Van Strien, 2001; Van Strien *et al.*, 2004, <http://www.ebcc.info/index.php?ID=516>). See <http://www.ebcc.info/pecbm.html> for further information on the various schemes (e.g. Szép & Nagy, 2002). Time series extended from 1990 to 2008 with a mean length of 15.05 years (SD = 3.8, min = 8, Table S3). The time series came from 18 countries, but growth rates estimates of two countries, Germany and Belgium, were further divided into two subregions and we ran additional analyses without either subregion to test for dependence on this historical artifact. Similar subdivisions of surveyed strata are used to assess population changes in the North American breeding bird survey (Sauer & Link, 2011).

Organismal attributes

We gathered life history, climatic, and habitat use attributes for all time series (Tables 1 and S2) with migratory and thermal niche attributes specified at the country level for each time series (henceforth population level) and dietary, body size, and farmland specialization attributes specified at the species level. Thermal coordinate (TC), an attribute measuring the position of a population within a species thermal range (Jiguet *et al.*, 2010b), was calculated using mean temperature in July (1981–2006) and 1 degree gridded European breeding ranges (Holt *et al.*, 2012). The index ranges between 1 and –1 with locations in warm parts of the breeding range having positive values and locations in cold parts having negative values (Fig. 1d). Breeding populations were classified as either permanent residents, short-distance migrants or long-distance migrants, following criteria in Both *et al.* (2010) and based on an extensive review of the literature (Fry *et al.*, 1986; Cramp *et al.*, 1994, Appendix S1). For populations exhibiting a mix of migratory strategies, the behavior involving the longest regularly travelled distance was used. We used a nominal categorization of species' specialization to farmland habitats (Farm, <http://www.ebcc.info/wpimages/other/SpeciesClassification2012.xls>) and scored species for their main breeding and winter diet type using categories of insectivores (*I*), herbivores (*H*), and species with a mixed or omnivorous diet (*O*). The assignment was based on multiple published data sets (Bohning-Gaese & Oberrath, 2003; Gregory *et al.*,

Table 1 Population, attribute, and environmental predictor variables used to explain population growth rates including context of the variables and the major predictions for their effects based on previous studies

Variable	Description and data source	Context and main predictions (<i>P</i>)
Population		
PopIndex	Indexed annual population abundance (N_t) – (PECBMS)	Accounts for density dependence of annual growth rates
Environment		
Cereal	Change in cereal yield from year $t-1$ to year t (FAOStat)	A surrogate for short-term agricultural intensification. <i>P</i> : Detrimental to farmland specialists and insectivores
SprProd	Annual spring (Mar-May) productivity anomaly in year t , estimated from NDVI (Pinzon <i>et al.</i> , 2005; Tucker <i>et al.</i> , 2005)	Spring resources and spring arrival. <i>P</i> : Beneficial to short-distance migrants, detrimental to long-distance migrants
SumTmp	Annual summer (Jun-Aug) temperature anomaly in year t (Mitchell & Jones, 2005)	Included for comparison with effects of winter and spring conditions
WinProd	Annual winter (Dec-Feb) productivity anomaly in the wintering range in year t , estimated from NDVI (Pinzon <i>et al.</i> , 2005; Tucker <i>et al.</i> , 2005)	A measure of the amount of resources in the African wintering range. <i>P</i> : Beneficial to long-distance migrants
WinTmp	Annual winter (Dec-Feb) temperature anomaly in year t (Mitchell & Jones, 2005)	A measure of how mild the winter is. <i>P</i> : Beneficial to permanent residents
Yield	Average cereal yield from 1990 to 2007 (FAOStat)	A surrogate for the general level of agricultural intensification. <i>P</i> : Detrimental to farmland specialists and insectivores
Attribute		
DietB	Species breeding diet; Insectivore (I), Herbivore (H), Omnivore (O) (Cramp <i>et al.</i> , 1994; Bohning-Gaese & Oberrath, 2003; Gregory <i>et al.</i> , 2007; Van Turnhout <i>et al.</i> , 2010; Holland <i>et al.</i> , 2012)	Accounts for differential effects of land use and climate change (see e.g. Cereal & Yield). Diet is correlated with migratory strategy and a competing predictor variable
DietW	Species winter diet; Insectivore (I), Herbivore (H), Omnivore (O) (see DietB)	See Diet B
Farm	Farmland specialization; specialist (Sp), nonspecialist (NSp) – (PECBMS)	Accounts for differential effects of agricultural intensification (see Cereal & Yield)
logBody	Logarithm of species body length (Bohning-Gaese & Oberrath, 2003)	Nuisance variable included to account for confounding trait variation
Migration	Migratory strategy; long-distance migrant (L), short-distance migrant (S), resident (R) – (this study, appendix S1)	Accounts for differential effects of weather and climate change (see respective variables). <i>P</i> : Long-distance migrants in decline
Region	Sub-Saharan wintering region (this study)	Accounts for differential effects of WinProd. <i>P</i> : Drier regions should show more positive effects
TC	Thermal coordinate, measures the position within the thermal range (Mitchell & Jones, 2005; Holt <i>et al.</i> , 2012)	<i>P</i> : Warmer (colder) populations should decline under weather and climate warming (cooling)
WHabitat	Habitat type in Sub-Saharan wintering range (Sanderson <i>et al.</i> , 2006; Heldbjerg & Fox, 2008)	<i>P</i> : WinProd effects in drier habitats should be more positive

2007; Van Turnhout *et al.*, 2010; Holland *et al.*, 2012) and a review of the standard literature (Cramp *et al.*, 1994). Finally, log-transformed average body length (logBody) was obtained from (Cramp *et al.*, 1994).

Environmental variables

We extracted environmental variables (Table 1) from populations' breeding and wintering ranges using a combination of (1) breeding country, (2) wintering range, (3) biomes of the breeding-, and (4) wintering range (Fig. S1). Population level wintering range estimates were based on references used for assigning migratory strategy (Fry *et al.*, 1986;

Cramp *et al.*, 1994; Appendix S1). We measured breeding area conditions in the seasons leading up to or during the breeding season by spatially intersecting breeding country and breeding biomes. We measured winter temperature (WinTmp), spring primary productivity (SprProd, also an indicator of spring earliness), and summer temperature (SumTmp). Furthermore, we measured winter conditions (primary productivity – WinProd) in the Sub-Saharan wintering ranges of long-distance migrants by intersecting wintering range and wintering biomes (Table S4). All variables were incorporated as annual anomalies through within subject mean centering (van de Pol & Wright, 2009). First we calculated the yearly mean within the intersected area from

original 0.5 degree maps (temperature variables) and 0.125 degree maps (primary productivity variables). We then converted the annual means to anomalies by subtracting a 26-year area mean (1981 – 2006) from the yearly means. Annual means in the wintering and breeding range were calculated in ArcGIS 9.3 (ESRI). The four bioclimatic variables have previously been used in the study of environmental change responses of breeding birds (Table S1, e.g. Peach *et al.*, 1998; Albright *et al.*, 2009; Jones & Cresswell, 2010; Schaub *et al.*, 2011). As a proxy for overall agricultural productivity, we used country level cereal yield (Cereal) obtained from the statistical database of FAO (<http://faostat.fao.org/>). This proxy has been used in previous studies looking at the effect of agricultural land use change on farmland birds (Donald *et al.*, 2001, 2006).

Statistical analysis

Long-term model. Regression models were constructed as linear mixed models with growth rates as response variable using the *lmer* function to optimize model log-likelihood via maximum likelihood approximation (as opposed to restricted maximum likelihood approximation, *lme4* 1.0-4 R-package <http://lme4.r-forge.r-project.org>). All continuous variables were transformed to mean zero and SD one to obtain estimates of standardized effect sizes. For the analysis of long-term population growth rates, we used the (log-scale) growth rate of the longest available time-series for each species-country combination between 1990 and 2008, corresponding to the additive TRIM slope ($R_{90,08}$). We considered species attributes and average cereal yield (1990–2007, Yield) as explanatory variables. The latter was included to describe the general level of agricultural intensification due to the likely nonlinear and lagged impacts of land use change at shorter time scales (Donald *et al.*, 2001). To account for confounding factors at the country level and species relatedness we included country (Jiguet *et al.*, 2010b) and nested taxonomic levels as random effects (Prinzing *et al.*, 2001; Jiguet *et al.*, 2010b). We tested two taxonomic random effect structures, one using just species identity and one nesting species within taxonomic family and order. Beyond accounting for country level confounding factors by incorporating country as random effect, we did not account for spatial autocorrelation per se. To account for uncertainty in growth rate estimates we conducted separate weighted and nonweighted analyses using the inverse standard errors of growth rate estimates as weights. Equation 1 shows the fixed effect structure of the full model for which all possible subset models were evaluated (variables as abbreviated above and in Table 1).

$$R_{90,08} \sim \text{Diet} * (\text{TC}, \text{Yield}, \text{Farm}) + \text{Migration} \\ * (\text{TC}, \text{Yield}, \text{Farm}) + \text{Farm} * \text{Yield} + \log \text{Body} + b_i + b_j + e \quad (1)$$

where parentheses delimit variables considered in interaction with a grouping variable (in total seven interactions). b_i and b_j are the respective random effects for country i and species j (nested within family and order) and e is the error term. We

evaluated the full model (eqn 1) using both breeding and wintering diet.

Short-term model. The aim of the short-term analysis was to investigate the effect of environmental conditions on (log-scale) annual population growth rates (the change in numbers from year t to $t + 1$, $R_{t,t+1}$). In particular, we were interested in comparing support for global change hypotheses generated from the long-term analysis. We therefore considered interactions between species attributes and environmental variables with the corresponding general formula (eqn 2):

$$R_{t,t+1} \sim \alpha + \beta_1 \text{PopIndex}_t + \beta_2 \text{Att} + \beta_3 \text{Env}_t + \beta_4 \text{Att} * \text{Env}_t \\ + b_i + b_j + e \quad (2)$$

where α is the intercept, β_{1-3} are parameters for main effects, β_4 is the parameter for a given attribute-environment interaction while b_i and b_j are the respective random effects for country i and population j (nested within species, family and order) and e is the error term. Inverse standard-errors of growth rate estimates were included as model weights. We further tested the robustness of consensus models (see model selection) to inclusion of year as a random factor in order to account for possible confounding environmental changes in a given year. Population index (PopIndex) was included to account for density dependence of annual growth rates and was standardized to mean zero and SD one for each time series and then jointly for all time series. Since conditions before and during breeding in year t can affect both the survival and reproductive components of recruitment in year $t + 1$, they should have a greater influence on population dynamics compared to conditions in-between breeding in year t and $t + 1$. We therefore focused on effects of weather and general vegetation conditions in year t and change in cereal yield from year $t-1$ to t . The rationale about relative influence of conditions in different years is expected to hold especially in species where offspring are recruited directly into the breeding population in the following breeding season (Cormont *et al.*, 2011). This is the case for all species in this analysis except for the corvids where breeding starts in the first to third year (Cramp *et al.*, 1994).

We evaluated all subsets of three full short-term models, with one of the fixed effect structures shown in Eqn (3):

$$R_{t,t+1} \sim \text{PopIndex}_t + \text{DietW} * (\text{Cereal}_{t-1,t}) + \text{Migration} \\ * (\text{WinTmp}_t, \text{SprProd}_t, \text{SumTmp}_t, \text{Cereal}_{t-1,t}) + \text{TC} \\ * (\text{WinTmp}_t, \text{SprProd}_t, \text{SumTmp}_t) + \text{Farm} * \text{Cereal}_{t-1,t} \\ + \log \text{Body} \quad (3)$$

where parentheses delimit interactions between multiple environmental variables and an attribute variable, variables are abbreviated as above and in Table 1. In the other two full models, we swapped the position of Migration and DietW in (3) to evaluate interactions between weather variables and breeding as well as wintering diet.

Model selection. We used the function *dredge* in the R-package MuMIn (<http://cran.r-project.org/web/packages/MuMIn/index.html>) to construct all possible subset models using AICc as selection criterion (Burnham & Anderson, 2002) and subsequently build consensus models containing variables overrep-

resented in the best model set. AICc measures assumed each random effect counting as one parameter and measured AICc sample size as the number of observations in the data set. Two criteria had to be fulfilled for model i to be included in the best model set.

- 1 $AICc[\text{model}_i] < (AICc[\text{Null}] - 4)$
- 2 $AICc[\text{model}_i] < (AICc[\text{Best}] + 4)$

where *Null* is the null model including only an intercept and *Best* is the model with lowest AICc score. To ensure that terms in the consensus model were not included due to large effects of other model terms, we applied the following criteria for inclusion of model term i in the consensus model, including criteria for its co-occurrence with model term j :

- 1 Corrected occurrence criteria: $(\text{frequency}[\text{term}_i \text{ in consensus set}] - \text{frequency}[\text{term}_i \text{ in full set}]) / (1 - \text{frequency}[\text{term}_i \text{ in full set}]) > 0.1$
- 2 Co-occurrence criteria: $\text{frequency}[\text{terms}_{i,j} \text{ co-occurring in consensus set}] > \text{frequency}[\text{terms}_{i,j} \text{ co-occurring in full set}]$

Model terms that fulfilled both criteria were included in the same consensus model while model terms that only fulfilled criterion 1 but not 2 were allocated into separate consensus models. We tested whether different cut-off values for criterion 1 (0, 0.02, 0.1) changed the results of the model selection (they rarely did) and used 0.1 as a final cut-off to focus on model terms with the largest overrepresentation in the best set.

Model parameters and confidence intervals were estimated with parametric bootstrapping build into the *bootMer* and *boot.ci* functions in the R-packages *lme4* 1.0-4 and *boot* 1.3-7, respectively (<http://cran.r-project.org/web/packages/boot/index.html>). Goodness-of-fit and model performance was evaluated by considering reduction in Penalized Weighted Residual Sums of Squares (PWRSS) (Pinheiro & Bates, 2000) as well as $\Delta AICc$ scores (Burnham & Anderson, 2002). The level of model collinearity was assessed using a kappa statistic for mixed-models (<https://github.com/aufrank/R-hacks/blob/master/mer-utils.R>) where values below 10 indicate low, values above 30 indicate high, and values in-between indicate moderate collinearity. All statistical analyses were carried out in R 2.15.3 64-bit (R Development Core Team, 2008).

Results

Long-term growth rates

Changes in the abundance of European farmland birds over the past two decades were best explained by a consensus model including migratory strategy (Migration) and breeding diet (DietB) as well as the covariates thermal coordinate (TC), long-term cereal yield (Yield), and body size (logBody, Fig. 2a, Table 2). More

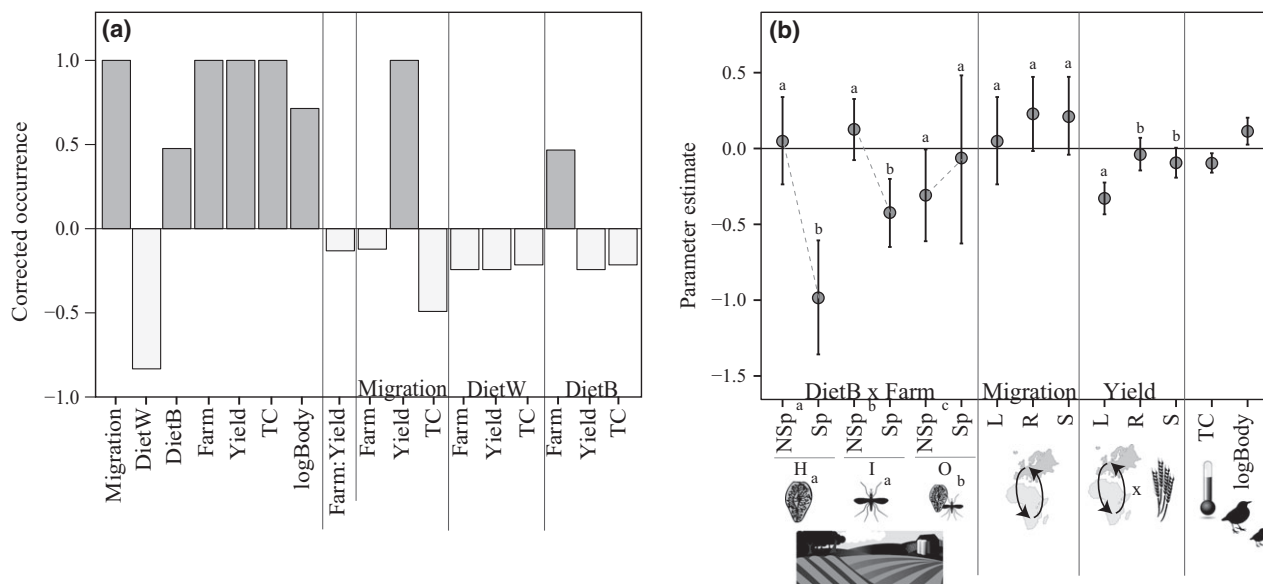


Fig. 2 Long-term population growth rates of common European breeding birds explained by attributes and long-term cereal yield in the consensus model. (a) Support for including attributes and long-term cereal yield in a consensus model that explain long-term population growth rates of 51 common European breeding birds. Model terms with corrected occurrence exceeding 0.1 were included in the consensus model. Corrected occurrence is shown for models including species and country as random effects, and inverse growth rate standard errors as weights (see methods for details). Colons indicate interacting variables. (b) Maximum likelihood parameter estimates and bootstrapped confidence intervals from the consensus model. Levels of grouping variables are invertebrate (*I*), herbivore (*H*), and mixed diet (*O*); long-distance migrant (*L*), permanent resident (*R*), and short-distance migrant (*S*); farmland specialist (*Sp*) and nonspecialist (*NSp*). If not otherwise specified, effects are parameterized assuming an herbivorous diet, long-distance migration and no farmland specialization. Continuous variables are parameterized at 1 SD and error bars are 95% confidence intervals. Symbols illustrate variables. Small letters indicate group contrast membership. Predictor variables abbreviated as in Table 1

Table 2 Properties of long-term growth rate models with the lowest AICc (*Best*), consensus model(s) (*Consensus*), and a model including only an intercept as fixed effect (*Null*). Where two models are identical only the bottom row contains information while the upper rows contains a dash. Model properties are: the Δ AICc-scores, the AICc weights within the shown model set (*AICc w*), the Penalized Weighted Residual Sums of Squares reduction with respect to *Null* (*PWRSS reduction*), the number of model parameters (*K*), the Kappa condition number (*Kappa*) and the fixed effect model terms (as defined in Table 1)

Weighting								
Random effects	Model	Δ AICc	AICc w	PWRSS reduction (%)	K	Kappa	Model terms	
Weighted								
Nested	Best	–	–	–	–	–	–	
	Consensus	0.00	1.00	2.32	20	13.71	Migration*Yield + Farm*DietB + TC + logBody	
	Null	36.76	0.00		6	1.00		
Species	Best	–	–	–	–	–	–	
	Consensus	0.00	1.00	2.38	16	11.77	Migration*Yield + Farm*DietB + TC + logBody	
	Null	36.41	0.00		4	1.00		
Nonweighted								
Nested	Best	0.00	0.53	1.98	20	13.71	Migration*Yield + Farm*Migration + Farm*DietB + TC + logBody	
	Consensus	0.27	0.47	2.01	18	11.77	Best - Farm*Migration	
	Null	33.93	0.00		6	1.00		
Species	Best	–	–	–	–	–	–	
	Consensus	0.00	1.00	2.02	16	11.77	Migration*Yield + Farm*DietB + TC + logBody	
	Null	34.03	0.00		4	1.00		

specifically, populations with high thermal coordinates had lowered growth rates (Fig. 2b, TC), as did populations in countries with higher cereal yield (Fig. 2b, Yield). In such high yield countries, growth rates of long-distance migrants (*L*) were lower compared to residents (*R*) and short-distance migrants (*S*; see Yield Fig. 2b). Farmland specialists (Farm; *Sp*) with herbivorous (*H*) or insectivorous diets (*I*) declined compared to nonspecialists (*NSp*) with similar diets (DietB \times Farm in Fig. 2b). In terms of model performance, Δ AICc values between consensus and null models were considerable, ranging between 33.9 and 36.4 (Table 2), while penalized weighted residual sums of squares (PWRSS, a goodness-of-fit measure) only were reduced slightly (min = 2.01%, max = 2.38%, Table 2). Model collinearity was in the low end of the moderate spectrum (Kappa: min = 11.77, max = 13.71) and all model terms had the same sign when tested one by one. Random effects explained between 0.3 and 12.4% of the total model variance and the species level tended to explain most of the variance among the taxonomical variables (Table S5).

Annual growth rates

All investigated environmental variables contributed to explain year-to-year change in abundance of European farmland birds (Figs 3 and S2, Table 3). In the consensus model, migratory strategy was the dominant explanatory attribute, interacting with every

environmental variable, whereas nonbreeding diet (DietW) only interacted with cereal yield (Cereal, Fig. S2a, Table 3). In-depth analyses confined to single migratory strategies in general corroborated results from the full model (Figs 3 and S3) and revealed further, more detailed patterns (Figs 4a–d and S2b–d). Each weather variable, for example, had a main effect on only one migratory strategy with the seasonal order of weather variables matching the order of breeding onset of migratory strategies (Fig. 4e). Thus, growth rates of residents increased after warm winters (WinTmp), short-distance migrants after more productive springs (SprProd), and growth rates of long-distance migrants increased after warm summers (SumTmp) (Fig. 4a–e). Positive effects of winter temperature and spring productivity increased in colder parts of species thermal ranges (interaction with TC in Fig. 4b,c). Populations of long-distance migrants wintering in central and eastern regions of Sub-Saharan Africa showed a positive response to increasing African winter primary productivity (WinProd, Fig. 4d). In this analysis, there was not support for including breeding winter temperature in the consensus model, but it featured in the single best model (Figs 4d and S4, Table 3).

To assess the robustness of model effects and contrasts to weather and yield changes across years we ran consensus models with year as a random variable. In the full model, all model effects and contrasts were identical to models without year as random effect in

Table 3 Characteristics of annual growth rate models for all studied European farmland birds (all) as well as subsets consisting of permanent residents (resident), short-distance migrants (short-distance), long-distance migrants (long-distance), and sub-Saharan long-distance migrants (Sub-Saharan). Properties are shown for the best model with the lowest AICc score (*Best*), the consensus model (*Consensus*), a model including only population index in year *t* as fixed effect (*Abundance*), and an intercept model (*Null*). Model properties are the Δ AICc scores (Δ AICc), the AICc weights within the shown set of models (AICc w), the reduction in Penalized Weighted Residual Sums of Squares in comparison to *Null* (PWRSS reduction), the number of model parameters (K), a measure of model collinearity (Kappa), and the fixed effect model terms (as defined in the text and Table 1). Dashes indicate that the best model equates the model in the below row

Strategy	Model	Δ AICc	AICc w	PWRSS			
				reduced (%)	K	Kappa	Fixed effects
All	Best	–	–	–	–	–	–
	Simplified consensus	0.0	0.83	17.37	22	6.72	Migration * WinTmp + Migration * SumTmp + Migration * Cereal + TC * SprProd + PopIndex
	Full consensus	1.8	0.17	17.32	28	9.77	<i>Simplified</i> + DietW * Cereal + Migration * SprProd
	Abundance	41.9	0.00	16.77	8	1.00	PopIndex
Long-distance	Null	1674.2	0.00	–	7	1.00	–
	Best	–	–	–	–	–	–
	Consensus	0.0	1.00	20.95	12	9.46	DietB * WinTmp + SumTmp + PopIndex
	Abundance	15.0	0.00	20.25	8	1.00	PopIndex
Short-distance	Null	597.0	0.00	–	7	1.00	–
	Best	0.0	0.67	17.20	11	1.24	TC * SprProd + PopIndex
	Consensus	1.5	0.33	17.41	16	4.39	<i>Best</i> + DietB * WinTmp
	Abundance	10.1	0.00	16.84	8	1.00	PopIndex
Resident	Null	566.1	0.00	–	7	1.00	–
	Best	–	–	–	–	–	–
	Consensus	0.0	1.00	19.11	19	3.47	DietW * SprProd + DietW * Cereal + TC * WinTmp + PopIndex
	Abundance	47.2	0.00	17.10	8	1.00	PopIndex
Sub-Saharan	Null	574.2	0.00	–	7	1.00	–
	Best	0.00	0.81	22.11	17	9.05	PopIndex + SumTmp + WinTmp + WinProd * Region
	Consensus	2.99	0.18	21.94	16	9.07	<i>Best</i> – WinTmp
	Abundance	9.56	0.01	21.21	8	1.00	PopIndex
Sub-Saharan	Null	540.87	0.00	–	7	1.00	–

the full model, indicating robustness of effects across years and little sensitivity to e.g. extreme events in a particular year (compare Figs 3 and S3 with Fig. S5–6). The same pattern was seen in the single strategy models where all contrasts and main effects had the same sign, with only minor changes in effect size (compare Fig. 4 with Fig. S7).

Population index (PopIndex) was the covariate with the largest effect size in all analyses (Figs 3–4 and S8). In comparison to null models, consensus models reduced PWRSS by 17–20%, mainly due to this large effect of population index (Table 3). Thus, attribute and environmental variables only reduced PWRSS by an additional 0.6–2% (Table 3). Individual random effects often explained less than 0.1% of the total variance and at maximum 4.8% (Table S6). Δ AICc values between consensus models and models including only population index ranged between 9.56 and 47.19 (Table 3).

Discarding either one of the German and Belgian subregions or varying the taxonomic random effects structure had no effect on model selection, parameter significance or sign of effects.

Discussion

We examined the potential for combined inference from decadal and annual time scales to broaden global change attribution of continental-scale changes in abundance of European farmland birds. The combined approach characterized the long-term demographic response to recent land-use and climate change and provided new insights with regard to the effect of annual weather fluctuations on short-term demographic responses that may aid pinpoint mechanisms underlying long-term global change responses. Long-term changes linked to species' specialization to farm-

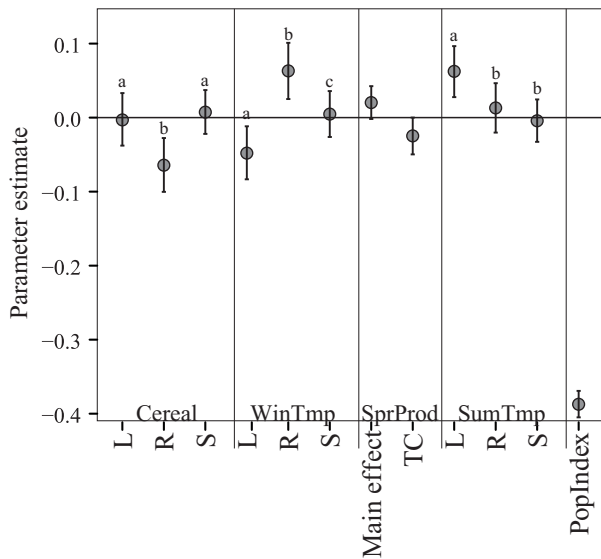


Fig. 3 Annual growth rates of common European breeding birds explained by attribute-environment interactions and population size in the previous year in a simplified consensus model including only the interactions with strongest support. Maximum likelihood parameter estimates and parametrically bootstrapped confidence intervals are presented. Migratory strategies are long-distance migrants (L), permanent residents (R) and short-distance migrants (S). All variables are parameterized at 1 SD and error bars are \pm 95% confidence intervals. Small letters indicate group contrast membership. Variables as abbreviated in Table 1.

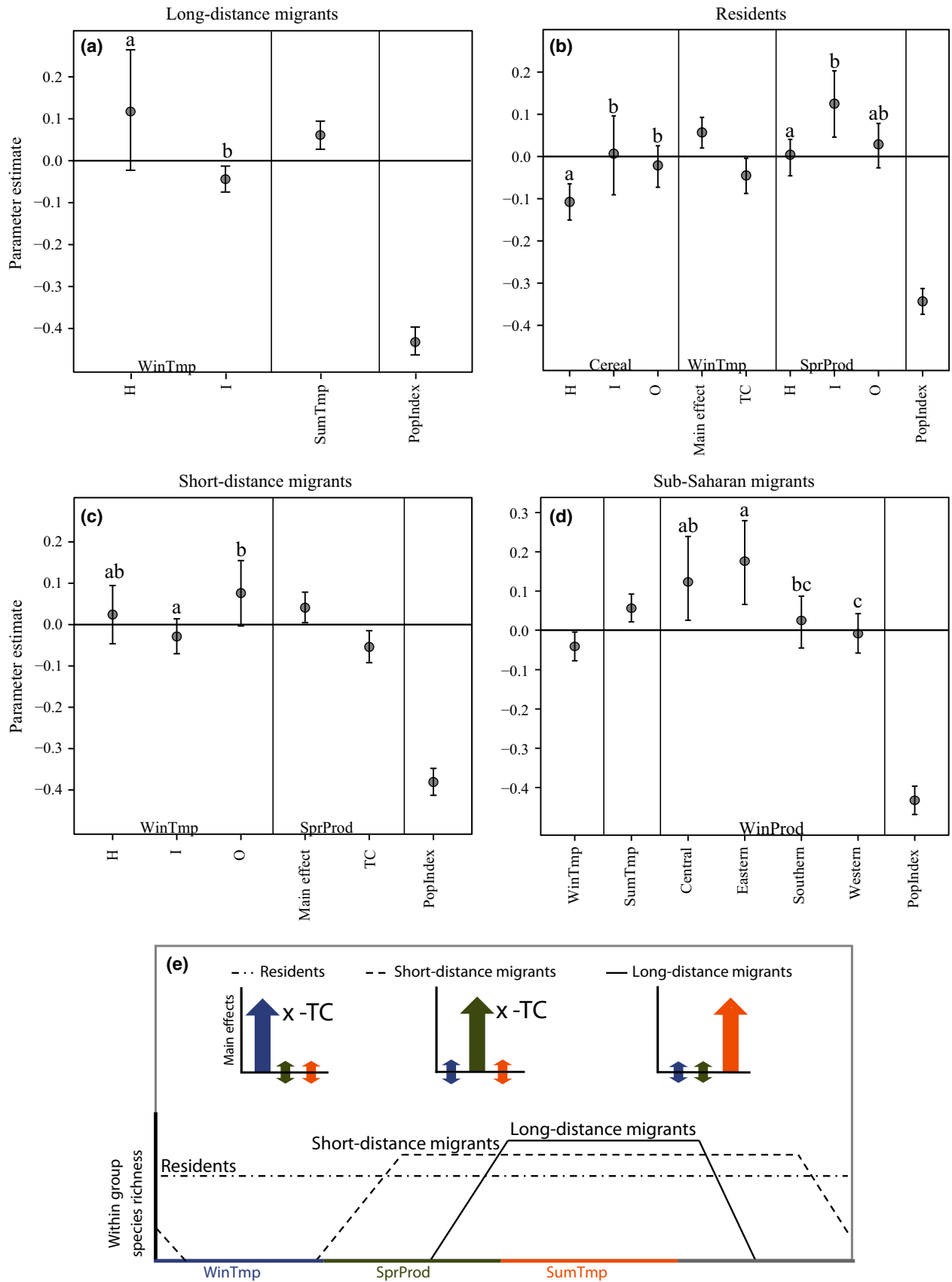
land habitat (Donald *et al.*, 2001, 2006; Voríšek *et al.*, 2010), climatic niche position (Jiguet *et al.*, 2010a,b) and movement strategy (Sanderson *et al.*, 2006) are not redundant, but occur simultaneously. Furthermore, short-term inference indicates that populations benefit from higher temperature or primary productivity leading up to or during their breeding season meaning that birds in the same location are influenced by bioclimatic variation in separate parts of the year. Populations of hot-dwelling species benefit more from winter and spring events which are predicted to increase in frequency with climate change, implying that long-term change in these weather variables could drive an

increase in more southerly distributed species (Gregory *et al.*, 2009).

Environmental correlates of short-term population change have the potential to yield insights into regulatory processes of populations and to help inform expectations for long-term outcomes under environmental change (Jiguet *et al.*, 2006). Yet, care must be taken before attempting to link the causes of change at a shorter time scale to drivers of change at a longer time scale. For example, although the 10-year mean temperature in Europe has increased since the 1990s, yearly seasonal conditions have been characterized by large fluctuations between years (European Environment Agency, 2012). Within the period of the present study, these fluctuations challenge direct extrapolation of short-term weather effects as drivers of long-term change. Despite this and the potential for various types of stochasticity as well as regional metapopulation processes to affect short-term dynamics even at large spatial scales (Tittler *et al.*, 2009), the short-term analysis help build expectations for the consequences of environmental change. Developing methods for projecting short-term environmental responses over longer time scales is an important focus for the future.

In line with previous studies we found that long-distance migrants are in relative decline (Sanderson *et al.*, 2006; Gregory *et al.*, 2007; Jiguet *et al.*, 2010a,b; Van Turnhout *et al.*, 2010), but only significantly so in countries with more intensive farmland practices (Fig. 2b). Migratory strategy is also the most important attribute in explaining annual weather effects (Figs 3 and 4). The positive effect of summer temperature on European long-distance migrants is known from two well-studied species (Crick, 2004; Jørgensen *et al.*, 2013), but has to our knowledge not been reported from multispecies studies. In the more arid central United States, Neotropical migrants are negatively affected by summer heat-waves in southern and montane areas, while they benefit from them further north (Albright *et al.*, 2011). In Europe, it is possible that long-distance migrants benefit from warmer summers in terms of higher reproductive performance from increased nestling survival, food availability, or competitive advan-

Fig. 4 Annual growth rates of (a) long-distance migrants, (b) permanent residents, (c) short-distance migrants and (d) Sub-Saharan long-distance migrants explained by attribute-environment interactions and population size in the previous year (PopIndex). Maximum likelihood parameter estimates and parametrically bootstrapped confidence intervals are presented. Levels of breeding (a, c) and nonbreeding diet (b) are herbivore (H), invertebrate (I), and mixed diet (O) and levels of Sub-Saharan wintering region (d) are central Africa (Central), eastern Africa (Eastern), southern Africa (Southern), western Africa (Western). All variables are parameterized at 1 SD and error bars are \pm 95% confidence intervals. (e) Bird populations are influenced by weather variation according to the general breeding phenology of their migratory strategy. Shown are the main effects of weather on growth rates of resident, short-distance migrant and long-distance migrants (large arrows in insets). A schematic of species richness in the breeding area over the course of the year is shown. Small letters indicate group contrast membership. Variables as abbreviated in Table 1.



tage (Crick, 2004; Jørgensen *et al.*, 2013). All else being equal, discrepancies in how climate change manifests at the respective times of breeding onset could contribute to the divergent long-term growth-rates observed between long-distance migrants and populations undertaking less extensive seasonal migrations.

Although we find that birds are affected by variation in the seasonal bioclimatic environment, we cannot distinguish from these analyses between a set of competing more proximate drivers. Limited power in separating competing proximate drivers may in particular be the case for the negative effect of milder non-breeding season weather on insectivorous long-distance migrants (Fig. 4a, Lemoine *et al.*, 2007; Cormont *et al.*, 2011). Here, direct effects of weather on physiology (Klaassen *et al.*, 2012), mismatches between populations and their food resources (Both *et al.*, 2006) and effects due to increased interspecific competition for food or nesting resources (Ahola *et al.*, 2007; Lemoine *et al.*, 2007) could all be acting simultaneously. Another challenge concerning long-distance migrants is evaluating the relative importance of conditions outside the breeding area (Sæther *et al.*, 2004). Interestingly, we find that winter temperature in the breeding area is less important when winter conditions in Africa are also considered. The effects of primary productivity in the central and eastern parts of Africa fits with expected negative consequences of drought (Baillie & Peach, 1992). Taken together, this speaks to a scenario where climate change in the European breeding areas might ultimately have mixed effects on long-distance migrants and for a balanced perspective on population regulation in the breeding vs. the wintering areas (the so-called 'tap' vs. 'tub' hypothesis, Sæther *et al.*, 2004), where environmental change in both areas have a regulating effect.

Indirect evidence that agricultural intensification is still negatively affecting farmland specialists is provided by our analysis, (Fig. 2b). However, we do not find evidence that farmland specialists in particular should be negatively affected by interannual changes in cereal yield (Figs 3–4). As noted, the effects of agricultural land-use change are complex and likely manifest with a longer temporal memory and lag than indicated by responses to annual yield changes. Cereal yield in Europe is influenced by environmental, mechanical, and genetic components (Brisson *et al.*, 2010) and changes in these components have different effects on farmland habitats, as experienced by birds. Despite the convincing evidence that abundance of farmland species is negatively associated with the general level of agricultural intensification (Donald *et al.*, 2001, 2006), the year-to-year effects of changing agricultural land-

use still needs further investigation at the continental scale.

Our analysis highlights the potential for using standardized multispecies surveys to integrate species attributes and environmental variables in combined attribution of global change responses across decadal and annual scales. This approach broadens the evidence base against which global change hypotheses are evaluated and we suggest that global change attribution will likely be improved by applying this combined time-scales perspective whenever annual time-series are available and when the aim is to link trends in long-term abundance to multiple environmental changes.

Acknowledgements

We wish to thank the many thousand volunteers who have contributed to the national monitoring schemes in Europe through the past four decades. This project was carried out in collaboration with the Pan-European Common Bird Monitoring Scheme and the European Bird Census Council. A big thank you goes out to the coordinators of the national schemes who kindly agreed to share valuable and unique data sets: Ainars Aunins, Åke Lindström, Alexander Mitschke, Andres Kuresoo, Anne Weiserbs, Dick Coombes, Elisabetta de Carli, Glenn Vermeersch, Henning Heldbjerg, Christian Vansteenwegen, Jaanus Elts, Jean-Paul Jacob, Jean-Yves Paquet, Johannes Schwarz, Juan Carlos del Moral, Kate Risely, Lorenzo Fornasari, Magne Husby, Markus Piha, Norbert Teufelbauer, Olivia Crowe, Renno Nellis, Risto Väisänen, Tibor Szep, Toni Laaksonen, Virginia Escandell. PV and IJB's contribution was part-funded by a core NGO operating grant from the European Commission to Stichting BirdLife Europe (both), and RSPB (PV). APT, CR, KT and PSJ acknowledge the Danish National Research Foundation for funding for the Center for Macroecology, Evolution and Climate.

References

- Ahola MP, Laaksonen T, Eeva T, Lehtikoinen E (2007) Climate change can alter competitive relationships between resident and migratory birds. *Journal of Animal Ecology*, **76**, 1045–1052.
- Albright TP, Pidgeon AM, Rittenhouse CD *et al.* (2009) Effects of drought on avian community structure. *Global Change Biology*, **16**, 2158–2170.
- Albright TP, Pidgeon AM, Rittenhouse CD, Clayton MK, Flather CH, Culbert PD, Radeloff VC (2011) Heat waves measured with MODIS land surface temperature data predict changes in avian community structure. *Remote Sensing of Environment*, **115**, 245–254.
- Araújo MB, Rahbek C (2006) ECOLOGY: how does climate change affect biodiversity? *Science*, **313**, 1396–1397.
- Araújo MB, Townsend Peterson A (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.
- Araújo M, Pearson R, Thuiller W, Erhard M (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. *Ecology Letters*, **14**, 484–492.
- Baillie SR, Peach WJ (1992) Population limitation in palearctic-African migrant passerines. *Ibis*, **134**, 120–132.
- Benton TG, Bryant DM, Cole L, Crick HQP (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology*, **39**, 673–687.

- BirdLife International (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status*. BirdLife International, Cambridge.
- Boatman ND, Brickle NW, Hart JD *et al.* (2004) Evidence for the indirect effects of pesticides on farmland birds. *Ibis*, **146**, 131–143.
- Bohning-Gaese K, Oberath R (2003) Macroecology of habitat choice in long-distance migratory birds. *Oecologia*, **137**, 296–303.
- Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.
- Both C, Van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1259–1266.
- Brisson N, Gate P, Gouache D, Charret G, Oury FX, Huard F (2010) Why are wheat yields stagnating in Europe? A comprehensive data analysis for France. *Field Crops Research*, **119**, 201–212.
- Brown CJ, Schoeman DS, Sydeman WJ *et al.* (2011) Quantitative approaches in climate change ecology. *Global Change Biology*, **17**, 3697–3713.
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. Springer, New York, NY.
- Butchart SHM, Walpole M, Collen B *et al.* (2010) Global biodiversity: indicators of recent declines. *Science (New York, N.Y.)*, **328**, 1164–1168.
- Clark JS, Carpenter SR, Barber M *et al.* (2001) Ecological forecasts: an emerging imperative. *Science*, **293**, 657–660.
- Collen B, Loh J, Whitmee S, McRae L, Amin R, Baillie JEM (2009) Monitoring change in vertebrate abundance: the living planet index. *Conservation Biology*, **23**, 317–327.
- Cormont A, Vos C, Van Turnhout C, Foppen R, Braak C (2011) Using life-history traits to explain bird population responses to changing weather variability. *Climate Research*, **49**, 59–71.
- Cramp S, Simmons KEL, Perrins CM (1994) *The Handbook of the Birds of Europe, North Africa and the Middle East*. Oxford University Press, Oxford.
- Crick HQP (2004) The impact of climate change on birds. *Ibis*, **146**, 48–56.
- Davey CM, Chamberlain DE, Newson SE, Noble DG, Johnston A (2011) Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, **21**, 568–578.
- Donald PF, Green RE, Heath MF (2001) Agricultural Intensification and the Collapse of Europe's Farmland Bird Populations. *Proceedings: Biological Sciences*, **268**, 25–29.
- Donald PF, Sanderson FJ, Burfield IJ, van Bommel FPJ (2006) Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture Ecosystems & Environment*, **116**, 189–196.
- European Environment Agency (2012) Global and European temperature (CSI 012/CLIM 001) - Assessment published Jun 2012.
- Fry CH, Keith S, Urban EK (1986) *The Birds of Africa, 7 Volumes*. Princeton University Press, Princeton.
- Green RE, Collingham YC, Willis SG, Gregory RD, Smith KW, Huntley B (2008) Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters*, **4**, 599–602.
- Gregory RD, van Strien A, Vorisek P, Meyling AWG, Noble DG, Foppen RPB, Gibbons DW (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **360**, 269–288.
- Gregory RD, Vorisek P, Van Strien A *et al.* (2007) Population trends of widespread woodland birds in Europe. *Ibis*, **149**, 78–97.
- Gregory RD, Willis SG, Jiguet F *et al.* (2009) An indicator of the impact of climatic change on European bird populations. *PLoS ONE*, **4**, e4678.
- Heldbjerg H, Fox T (2008) Long-term population declines in Danish trans-Saharan migrant birds. *Bird Study*, **55**, 267–279.
- Hilden O (1989) The effect of severe winters on the bird fauna of Finland. *Memoranda Societatis pro Fauna et Flora Fennica*, **65**, 59–66.
- Holland JM, Smith BM, Birkett TC, Southway S (2012) Farmland bird invertebrate food provision in arable crops. *Annals of Applied Biology*, **160**, 66–75.
- Holt BG, Lessard J-P, Borregaard MK *et al.* (2012) An update of Wallace's zoogeographic regions of the world. *Science*, **339**, 74–78.
- Huntley B, Collingham YC, Willis SG, Green RE (2008) Potential impacts of climatic change on European breeding birds. *PLoS ONE*, **3**, e1439.
- Jiguet F, Julliard R, Thomas CD, Dehorter O, Newson SE, Couvet D (2006) Thermal range predicts bird population resilience to extreme high temperatures. *Ecology Letters*, **9**, 1321–1330.
- Jiguet F, Gregory RD, Devictor V, Green RE, Vorisek P, Van Strien A, Couvet D (2010a) Population trends of European common birds are predicted by characteristics of their climatic niche. *Global Change Biology*, **16**, 497–505.
- Jiguet F, Devictor V, Ottvall R, Van Turnhout C, Van der Jeugd H, Lindström Å (2010b) Bird population trends are linearly affected by climate change along species thermal ranges. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 3601–3608.
- Jones T, Cresswell W (2010) The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? *Journal of Animal Ecology*, **79**, 98–108.
- Jørgensen PS, Tottrup AP, Rahbek C, Geertsma M (2013) Effects of summer weather on reproductive success of the Red-backed Shrike (*Lanius collurio*). *Bird Study*, **60**, 1–10.
- Klaassen M, Hoyer BJ, Nolet BA, Buttemer WA (2012) Ecophysiology of avian migration in the face of current global hazards. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **367**, 1719–1732.
- Knudsen E, Lindén A, Both C *et al.* (2011) Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, **86**, 928–946.
- LaDeau SL, Kilpatrick AM, Marra PP (2007) West Nile virus emergence and large-scale declines of North American bird populations. *Nature*, **447**, 710–713.
- Lande R, Engen S, Saether B-E (2003) Stochastic population dynamics in ecology and conservation. In: *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, New York, NY, USA.
- Lemoine N, Schaefer HC, Bohning-Gaese K (2007) Species richness of migratory birds is influenced by global climate change. *Global Ecology and Biogeography*, **16**, 55–64.
- Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology*, **25**, 693–712.
- Newton I (1998) Bird conservation problems resulting from agricultural intensification in Europe. In: *Avian Conservation: Research and Management* (eds Marzluff JM, Sallabanks R), p. 563. Island Press, Washington, DC, USA.
- Newton I (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis*, **146**, 579–600.
- Niemi GJ, McDonald ME (2004) Application of ecological indicators. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 89–111.
- Pannekoek J, Van Strien A (2001) *TRIM 3 Manual. Trends and Indices for Monitoring Data. Paper no. 0102*. Statistics Netherlands, Voorburg, the Netherlands.
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Parmesan C, Duarte C, Poloczanska E, Richardson AJ, Singer MC (2011) Overstretching attribution. *Nature Climate Change*, **1**, 2–4.
- Parmesan C, Burrows MT, Duarte CM, Poloczanska ES, Richardson AJ, Schoeman DS, Singer MC (2013) Beyond climate change attribution in conservation and ecological research. *Ecology Letters*, **16**, 58–71.
- Peach WJ, Baillie SR, Balmer DE (1998) Long-term changes in the abundance of passerines in Britain and Ireland as measured by constant effort mist-netting. *Bird Study*, **45**, 257–275.
- Pinheiro JC, Bates DM (2000) *Mixed-Effects Models in S and S-Plus*. Springer, New York.
- Pinzon J, Brown ME, Tucker CJ (2005) Satellite time series correction of orbital drift artifacts using empirical mode decomposition. In: *Hilbert-Huang Transform: Introduction and Applications* (eds Huang N, Shen S), pp. 167–186. World Scientific Publishing Co., Singapore.
- van de Pol M, Wright J (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, **77**, 753–758.
- Prinzing A, Durka W, Klotz S, Brandl R (2001) The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings. Biological Sciences/The Royal Society*, **268**, 2383–2389.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Development Core Team, Vienna.
- Saether BE, Tufto J, Engen S, Jerstad K, Rostad OW, Skatan JE (2000) Population dynamical consequences of climate change for a small temperate songbird. *Science*, **287**, 854–856.
- Saether BE, Sutherland WJ, Engen S (2004) Climate influences on avian population dynamics. In: *Birds and Climate Change* (eds Møller AP, Fielder W, Berthold P), pp. 185–209. Academic Press Ltd, London.
- Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, van Bommel FPJ (2006) Long-term population declines in Afro-Palaearctic migrant birds. *Biological Conservation*, **131**, 93–105.
- Sauer JR, Link WA (2011) Analysis of the North American breeding bird survey using hierarchical models. *Auk*, **128**, 87–98.
- Schaub M, Jakober H, Stauber W (2011) Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine. *Oecologia*, **167**, 445–459.

- Scholes RJ, Mace GM, Turner W *et al.* (2008) Ecology. Toward a global biodiversity observing system. *Science (New York, N.Y.)*, **321**, 1044–1045.
- Szép T, Nagy K (2002) *Mindennapi Madaraink Monitoringja (MMM) 1999–2000*. Magyar Madártani és Természetvédelmi Egyesület, Budapest.
- Ter Braak CJF, van Strien AJ, Meijer R, Verstrael TJ (1994) Analysis of monitoring data with many missing values: which method? (eds Hagemeyer EJM, Verstrael TJ). *Proceedings of the 12th International Conference of IBCC and EOAC*, pp. 663–673.
- Thorup K, Tottrup AP, Rahbek C (2007) Patterns of phenological changes in migratory birds. *Oecologia*, **151**, 697–703.
- Tittler R, Villard M-A, Fahrig L (2009) How far do songbirds disperse? *Ecography*, **32**, 1051–1061.
- Tucker CJ, Pinzon JE, Brown ME *et al.* (2005) An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. *International Journal of Remote Sensing*, **26**, 4485–4498.
- Van Strien AJ, Pannekoek J, Hagemeyer W, Verstrael T (2004) A loglinear Poisson regression method to analyse bird monitoring data. (ed Anselin A). *Proceedings of the International Conference and 13th Meeting of the European Bird Census Council*, **13**, pp. 33–39.
- Van Turnhout CAM, Foppen RPB, Leuven RSEW, Van Strien A, Siepel H (2010) Life-history and ecological correlates of population change in Dutch breeding birds. *Biological Conservation*, **143**, 173–181.
- Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein F, Škorpilová J, Gregory RD (2013) The decline of Afro-Palaeartic migrants and an assessment of potential causes (ed Fox T). *Ibis*, **156**, 1–22.
- Vorišek P, Jiguet F, van Strien A, Škorpilová J, Klvanová A, Gregory RD (2010) Trends in abundance and biomass of widespread European farmland birds: how much have we lost? In: *BOU Proceedings - Lowland Farmland Birds III*, pp. 1–24. BOU Proceedings – Lowland Farmland Birds III.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Literature used to identify population migratory strategies and wintering ranges.

Table S1. Characteristics of recent multispecies studies examining temporal bird population trends in relation to land use and climate change at a large spatial scale.

Table S2. Attributes and other species characteristics.

Table S3. Temporal extent of growth rate time series.

Table S4. Wintering region and wintering habitat for Sub-Saharan long-distance migrants.

Table S5. Explanatory ability of random effect variables in the analysis of long-term growth rates.

Table S6. Explanatory ability of random effect variables in the analysis of annual growth rates.

Figure S1. A map of areas used to designate wintering ranges and migratory strategies.

Figure S2. Corrected occurrence of environmental variables and attribute-environment interactions in the best set of annual growth rate models.

Figure S3. Parameter estimates in the full consensus model of annual growth rates.

Figure S4. Corrected occurrence of environmental variables and attribute-environment interactions in the best set of annual growth rate models for Sub-Saharan long-distance migrants.

Figure S5. Parameter estimates in the simplified consensus model of annual growth rates including year as random factor.

Figure S6. Parameter estimates in the full consensus model of annual growth rates including year as random factor.

Figure S7. Parameter estimates in single migratory strategy consensus models of annual growth rates including year as random factor.

Figure S8. Negative density dependence in common European breeding birds.