

LETTER

Assessing the Performance of EU Nature Legislation in Protecting Target Bird Species in an Era of Climate Change

Fiona J. Sanderson¹, Robert G. Pople², Christina Ieronymidou², Ian J. Burfield², Richard D. Gregory¹, Stephen G. Willis³, Christine Howard³, Philip A. Stephens³, Alison E. Beresford¹, & Paul F. Donald¹

¹ RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

² BirdLife International, Wellbrook Court, Girton Road, Cambridge, CB3 0NA, UK

³ School of Biological and Biomedical Sciences, Durham University, South Road, Durham, DH1 3LE, UK

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Correspondence

Paul F. Donald, RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire SG19 2DL, UK. phone: +44 (0)1767 680551; fax: +44 (0)1767 692365
E-mail: paul.donald@rspb.org.uk

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Abstract

International legislation forms a cornerstone of conservation, yet its efficacy is rarely quantified. We assess whether species listed on Annex I of the European Union (EU) Birds Directive, for which EU Member States are obliged to implement special conservation measures, differ systematically in their short-term (2001–2012) or long-term (1980–2012) population trends from those of non-Annex I species. In both periods, Annex I species had more positive trends than non-Annex I species, particularly in countries that joined the EU earlier. There were additional signatures of climate change and life history strategy in the trends of species in one or both periods. Within Annex I species, long-distance migrants fared significantly worse than other species, suggesting that enhanced protection on the breeding grounds alone may be insufficient for these species. We conclude that the EU's conservation legislation has had a demonstrably positive impact on target species, even during a period in which climate change has significantly affected populations.

Introduction

The loss of biodiversity is seen increasingly as a political problem that requires political solutions, with legislation being the main route of delivery (Boere & Rubeck 2002). Yet it is remarkably difficult to assess the impacts of international conservation legislation, as their targets tend not be quantitative (and therefore testable), and data on the responses of the target species may be lacking (Ferraro & Pattanayak 2006; Miteva *et al.* 2012). This is increasingly important as climatic change increasingly influences wildlife populations (e.g., Jiguet, Gregory *et al.* 2010; Chen *et al.* 2011), since the ability of largely static international conservation legislation to mitigate such effects is practically unknown (Trouwborst 2009; Pearce-Higgins & Green 2014).

Many environmental, ecological, and political drivers of trends in European bird populations have been identified, including habitat (Donald *et al.* 2006; Gregory *et al.*

2007), migration strategy (Sanderson *et al.* 2006; Vickery *et al.* 2014), and niche breadth (Le Viol *et al.* 2012). A clear signature of climate change is also apparent, with species typical of warmer habitats generally doing better across Europe than cold-adapted species (Gregory *et al.* 2009; Jiguet, Gregory *et al.* 2010; Pearce-Higgins & Green 2014).

Monitoring has also identified strong political drivers of bird population change in Europe, demonstrating, for example, the impacts on birds of European Union (EU) agricultural policy (Donald *et al.* 2006; Butler *et al.* 2010) and EU nature conservation legislation (European Commission 2010; Pellissier *et al.* 2013; Santana *et al.* 2013; Kolecek *et al.* 2014). The 1979 EU Birds Directive (2009/147/EC) places an obligation on all EU Member States to protect their wild birds, with an emphasis on migratory species and Annex I species (European Union 2009). Species listed on Annex I, for which Member States must implement “special conservation mea-

tures", fared significantly better as a group between 1990 and 2000 than non-Annex I species (Donald *et al.* 2007). By 2012, around 40% of the EU's regularly breeding species were listed on Annex I, or had subspecies listed on Annex I.

We use a new data set of both long-term (1980-2012) and short-term (2001-2012) trends in the populations of all breeding bird species occurring naturally in the EU to assess whether previous evidence of a positive impact of the Birds Directive is supported by more recent, and longer term, data from a greatly enlarged EU. We simultaneously assess the contribution of climate change susceptibility and other species-level traits as predictors of these trends, and assess whether, once these are controlled, the Birds Directive has an independent explanatory effect. This is the first attempt to quantify the impacts of international conservation legislation while simultaneously incorporating the effects of climatic change.

Methods

Data collection and collation

We analyzed a recently available data set on national bird population trends of all regularly breeding species across the EU (http://bd.eionet.europa.eu/activities/Reporting/Article_12/Reports_2013/Member_State_Deliveries). These data were largely collected as part of a process that requires each EU Member State to report on progress toward national implementation of the Birds Directive (Article 12, EU Birds Directive). Reports were submitted in 2013-2014 and followed defined guidelines (N2K Group 2011). No data were received for Greece, and the Czech Republic reported on only a small subset of taxa; missing data for these countries were filled using data collected by the national partners of the BirdLife International network following the same data collection protocol. Croatia did not join the EU until 2013 and so did not report for this period, leaving data from 27 EU countries in the analyses. We excluded data from the Canary Islands, Madeira, the Azores, and Gibraltar, which contained many missing values.

We followed the taxonomy of BirdLife International (2015). Reporting was undertaken at species level, with a few exceptions (Appendix S1). We excluded non-native species from the analyses as these are not covered by the Birds Directive.

Member States were required to report population size and trends for two periods, short-term (2001-2012) and long-term (1980-2012), for all regularly occurring breeding species. For each species-by-country estimate of population size and trend, respondents were asked to record the method by which the estimate was derived

(1 = expert opinion with no or minimal sampling; 2 = estimate based on partial data with some extrapolation and/or modeling; 3 = complete survey or a statistically robust estimate). For population size estimates, respondents were asked to record the number of breeding pairs (or occasionally other units) with estimates of minima and maxima according to a range of criteria (from a single minimum estimate to 95% CLs). For both long- and short-term trend estimates, respondents were asked to record the magnitude (as a single percentage change or as a range of minimum and maximum estimates of percentage change) of the trends plus the start and end years of the trend period if it differed from the standard 12- or 33-year periods. In all cases, the sources of the data were recorded. For analysis, we used the geometric mean of minimum and maximum estimates of percentage change, and where the population trend was recorded as fluctuating around zero (stability), we assumed it to be zero.

Systematic long-term annual monitoring data, which can be truncated to precise time intervals to fit the two predefined recording periods, are not available for all species in all countries, and in many cases the data used were drawn from a wide range of other sources, such as shorter-term annual monitoring schemes, or trends derived from two or more censuses that may not precisely coincide with the reporting periods. We discarded population trends if they did not overlap the monitoring period by at least half the specified period. Where the monitoring period provided in the database differed from that of the specified time period, we extrapolated trends to the correct time period using the methodology of the IUCN Red List (IUCN 2014), assuming a constant exponential rate of change and the annual rate of change (λ) calculated as

$$\lambda = (\text{total change})^{(1/t)}$$

where t = monitored time period. Whatever the provenance of the data submitted, any trends from the highest quality data (weight of 3) that had to be extrapolated to the prescribed reporting periods were assigned a data quality weight of 2 in the models.

Population trends, originally expressed in percentages, were rescaled to $\ln(\text{proportional change})$, resulting in trends with either a halving or a doubling of the population being equivalently distributed around zero (Gregory *et al.* 2005).

Of the 5,642 valid species-by-country combinations, including data on 415 species, data on the magnitude of trend were received for 3,789 (67.2%) long-term trends and 4,425 (78.4%) short-term trends. Because Annex I species may be more likely to have reported trends due to reporting requirements, we assessed the influence

of missing data on our analyses by imputing missing values with chained equations, using the “mice” package 2.22 (Buuren & Groothuis-Oudshoorn 2011) in R 3.1.2 (R Development Core Team 2013) and running the same explanatory model sets on these data (Appendix S2). As models derived from imputed data sets did not differ qualitatively with respect to Annex I status from those derived from the raw data with missing values, we present only models of the raw data.

Explanatory variables

Because population trends of birds in the EU may vary between species in different habitats (e.g. Donald *et al.* 2006), with different migration strategies (e.g. Sanderson *et al.* 2006) or with different population sizes (e.g. Inger *et al.* 2015), we included variables to control for these main effects in the models, excluding potential explanatory covariates that were confounded with these (Zuur *et al.* 2009; Appendix S3). To control for the potential effect of life history traits on population trend (Jiguet *et al.* 2007), we also fitted measures of generation length and clutch size as explanatory covariates. The explanatory variables fitted to the models are listed in Table 1.

For each species, we estimated a climate suitability trend (CST), a measure of the likely response of each species' range to climate change for each of the two time periods following the methods of Gregory *et al.* (2009) and Bagchi *et al.* (2013). A species' CST is the slope of a regression of the logit of modeled mean annual climate suitability across the species' range against time. Derivation of a CST requires first that species' occurrence data are related to climate data taken from a relevant period (typically a 30-50-year mean climate preceding or covering the period of species range data collection). Species distribution models (SDMs) are used to link the two. These SDMs are then applied to annual climate data to produce annual probabilities of occurrence (sometimes termed climate suitability), which can be regressed on time. A positive CST indicates that the species is expected to expand in range (and by implication in population) given the observed changes in climate, whereas a negative CST indicates predicted range contraction. Full details of the methods used to estimate CST are given in Appendix S4.

We fitted Annex I status to the models in two ways. First, we created a covariate for each species-by-country combination that reflected the number of years (by 2012) that the respective species had been on Annex I or the number of years that the respective country had been in the EU, whichever was lower. Species never added to Annex I received a value of zero. However, because this covariate was strongly bimodal, with most values being

zero (i.e., never on Annex I) or over 20 (i.e., listed on Annex I since 1979), we also fitted Annex I status as a binary factor reflecting whether or not each species had been on Annex I for at least 6 years by 2012 (half the short-term reporting period, to allow for time lags in population trends responding to protection under Annex I). These models also included a 2-level factor separating countries from the original EU15 (EU_{old}) from those joining the EU in or after 2004 (EU_{new}).

Data analysis

Visual inspection showed that population trends were normally distributed, so we fitted linear mixed models to population trends using the package “lme4” (Bates *et al.* 2014) in R 3.1.2 (R Development Core Team 2013). As trends within countries and species are unlikely to be independent, we fitted species and country as random effects. In order to account for possible non-independence in the trends of closely related species, Family was nested within Order (using the higher-level taxonomy of BirdLife International 2015), and fitted as a random effect (following Jiguet, Devictor *et al.* 2010). Where subspecies were listed on Annex I, only the relevant country-level populations of these subspecies were recorded as being on Annex I.

As all Member States must take conservation measures for Annex I species, the appropriate test of whether the Birds Directive has been effective is whether population trends of Annex I species are more positive than those of non-Annex I species across all Member States, rather than whether the total EU population is increasing, since the latter could occur through an increase in the population in one country with a large population even if smaller populations elsewhere were all in decline. Our response variable for each time period was therefore the trend of each species in each country, which we weighted by a measure of the method used to collect the data (see above), effectively a measure of data quality. This weighting yielded results that were qualitatively the same as analyses undertaken without weighting.

To test whether the impact of conservation action in Europe resulting from Annex I listing differed between species resident in Europe throughout the year and species resident elsewhere (usually Africa) for part of the year, we fitted an interaction between migration strategy and Annex I status.

We used the “dredge” function in the R package “MuMIn” (Bartoń 2012) to fit all possible models ($n = 416$ for model sets fitted with a binary Annex I factor and $n = 320$ for model sets fitted with years on Annex I fitted as a continuous variable). We fitted interaction terms only if both main variables were already present in

Table 1 Explanatory variables fitted to the models and their sources

Variable	Type	Description and source
Main habitat association (<i>Hab</i>)	9-level factor	A categorical primary habitat association classification based upon data in Tucker and Evans (1997) as applied by Donald <i>et al.</i> (2006) and Sanderson <i>et al.</i> (2006): (1) marine; (2) coastal; (3) inland wetland; (4) tundra, mires, and moorland; (5) boreal and temperate forests; (6) Mediterranean forest, shrubland, and rocky habitats; (7) agricultural and grassland; (8) montane grassland; and (9) nonspecialist.
Migration strategy (<i>Mig</i>)	2-level factor	Condensed from the 5-level factor used by Sanderson <i>et al.</i> (2006) to a 2-level factor indicating whether a species is a long-distance migrant to sub-Saharan Africa or southern Asia, or not.
Climate suitability trend (<i>CST</i>)	Covariate	A prediction of each species' likely responses to climate change over each of the two trend periods. See Appendix S2 for full details.
Annex I (<i>A1</i>)	Covariate	The number of years each species (by country) had been on Annex I by 2012—from either the year the species was added to the Annex or the year that country joined the EU, whichever is the shorter. For non-Annex I species, the number is set to zero.
	2-level factor	A binary factor relating to whether or not a species had been listed on Annex I for at least 6 years by 2012 (see text).
EU designation (<i>EU</i>)	2-level factor	A binary factor indicating whether or not the respective country joined the EU after 2003 (see text).
Population size ($\ln(\text{pop})$)	Covariate	Natural log of the population size of each species in each country.
Generation length ($\ln(\text{gen length})$)	Covariate	Natural log of the generation length of each species (data from BirdLife International 2015). Data were centred around zero to avoid collinearity with the model intercept (Zuur <i>et al.</i> 2009).
Mean clutch size (<i>Clutch size</i>)	Covariate	Mean clutch size of each species (data from BirdLife International 2015). Data were centred around zero to avoid collinearity with the model intercept (Zuur <i>et al.</i> 2009).

Variable codes in parentheses indicate those used in Table 2.

the model. Model fit was estimated using maximum likelihood to compare models with differing fixed variables, with models compared using AIC_c (Burnham & Anderson 2002), with the final best supported model(s) (those with $\Delta AIC_c < 2$; Burnham & Anderson 2002) refitted using restricted maximum likelihood (REML; Zuur *et al.* 2009). We plotted residuals of all best supported models against fitted values and explanatory variables included and excluded from the models to confirm that there were no unexplained patterns in the residuals (Zuur *et al.* 2009).

Results

Systematic differences between Annex I and non-Annex I species

We first used univariate χ^2 tests and ANOVA to assess systematic differences between Annex I and non-Annex I species in the explanatory variables to aid model interpretation. There was no systematic difference between Annex I and non-Annex I species in main habitat association ($\chi^2_8 = 14.41$, $P = 0.07$) or in migration strategy ($\chi^2_1 = 0.53$, $P = 0.47$). Annex I species were significantly nonrandomly distributed across taxonomic Orders ($\chi^2_{22} = 114.4$, $P < 0.0001$), residuals indicating a higher than

expected proportion of Annex I species in the Orders Accipitriformes, Procellariiformes and Pelecaniformes, and a lower proportion in the large Order Passeriformes. As a result, Annex I species had significantly longer generation length ($F_{1,451} = 29.9$, $P < 0.0001$) and lower mean clutch size ($F_{1,451} = 12.4$, $P < 0.0001$) than non-Annex I species.

Predictors of short-term (2001-2012) trends

The only predictors whose regression coefficients differed significantly from zero in the best supported models of short-term population trend were Annex I status (whether fitted as a covariate or as a binary factor; in both cases Annex I status had a positive effect), generation length and a positive effect of the log of population size (Table 2, Panels A and B; Figure 1a, b). Migration strategy had no significant effect alone, but its presence in the best supported models was due to a highly significant interaction between Annex I status and migration strategy, indicating that long-distance (largely Afro-Palaearctic) Annex I migrants had trends that did not differ from those of non-Annex I migrants (Figure 2a). A significant negative interaction between Annex I status when fitted as a binary variable and “old” and “new” EU

Table 2 Parameter estimates (PEs) derived for the best supported models ($\Delta AIC_c < 2$) in each set of models, using REML, with standard errors (SEs) in parentheses

	A1	Mig	ln(pop)	EU	CST	ln(gen length)	Clutch size	A1*Mig	A1*EU	AIC _c weight	ΔAIC_c
Panel A: Short-term trends (2001-2012), years on Annex I as covariate											
Model 1	0.010 (0.002)	0.006 (0.047)	0.015 (0.003)	0.084 (0.060)		0.171 (0.060)		-0.009 (0.003)	n/a	0.13	0
Model 2	0.009 (0.002)	0.008 (0.047)	0.015 (0.003)			0.171 (0.060)		-0.009 (0.003)	n/a	0.13	0.04
Model 3	0.009 (0.002)	0.002 (0.048)	0.015 (0.003)		1.437 (1.204)	0.179 (0.060)		-0.009 (0.003)	n/a	0.10	0.64
Model 4	0.009 (0.002)	0.001 (0.048)	0.015 (0.003)	0.083 (0.060)	1.414 (1.203)	0.178 (0.060)		-0.008 (0.003)	n/a	0.10	0.64
Model 5	0.009 (0.002)	0.003 (0.047)	0.015 (0.003)	0.084 (0.060)		0.146 (0.067)	-0.010 (0.012)	-0.008 (0.003)	n/a	0.07	1.42
Model 6	0.009 (0.002)	0.005 (0.048)	0.015 (0.003)			0.146 (0.067)	-0.010 (0.012)	-0.009 (0.003)	n/a	0.07	1.43
Model 7	0.009 (0.002)	-0.001 (0.048)	0.015 (0.003)		1.467 (1.205)	0.153 (0.068)	-0.010 (0.012)	-0.008 (0.003)	n/a	0.05	1.97
Model 8	0.009 (0.002)	-0.002 (0.048)	0.015 (0.003)	0.083 (0.060)	1.444 (1.205)	0.153 (0.068)	-0.010 (0.012)	-0.008 (0.003)	n/a	0.05	2.00
Panel B: Short-term trends (2001-2012), presence on Annex I as binary factor											
Model 1	0.299 (0.052)	0.065 (0.050)	0.015 (0.003)	0.093 (0.061)		0.176 (0.060)		-0.322 (0.075)	-0.146 (0.043)	0.32	0
Model 2	0.289 (0.053)	0.060 (0.051)	0.015 (0.003)	0.093 (0.061)	1.181 (1.208)	0.182 (0.060)		-0.316 (0.075)	-0.144 (0.043)	0.19	1.07
Model 3	0.293 (0.053)	0.061 (0.051)	0.015 (0.003)	0.093 (0.061)		0.154 (0.067)	-0.008 (0.012)	-0.317 (0.075)	-0.146 (0.043)	0.15	1.54
Panel C: Long-term trends (1980-2012), years on Annex I as covariate											
Model 1	0.025 (0.004)	-0.200 (0.100)	0.058 (0.007)		15.375 (4.505)	0.275 (0.155)	-0.050 (0.029)	-0.013 (0.005)	n/a	0.19	0
Model 2	0.025 (0.004)	-0.203 (0.100)	0.059 (0.007)	0.174 (0.137)	15.311 (4.503)	0.277 (0.155)	-0.050 (0.029)	-0.013 (0.005)	n/a	0.16	0.34
Model 3	0.026 (0.004)	-0.186 (0.100)	0.058 (0.007)		15.638 (4.514)	0.404 (0.137)		-0.013 (0.005)	n/a	0.12	0.99
Model 4	0.025 (0.004)	-0.242 (0.099)	0.058 (0.007)		15.347 (4.526)		-0.074 (0.026)	-0.013 (0.005)	n/a	0.11	1.11
Model 5	0.026 (0.004)	-0.186 (0.100)	0.058 (0.007)		15.638 (4.514)	0.404 (0.137)		-0.013 (0.005)	n/a	0.10	1.26
Model 6	0.026 (0.004)	-0.245 (0.099)	0.059 (0.007)	0.172 (0.136)	15.283 (4.524)		-0.074 (0.026)	-0.012 (0.005)	n/a	0.09	1.49
Panel D: Long-term trends (1980-2012), presence on Annex I as binary factor											
Model 1	0.702 (0.111)	-0.052 (0.109)	0.058 (0.007)	0.182 (0.139)	16.147 (4.507)	0.291 (0.155)	-0.050 (0.029)	-0.582 (0.156)	-0.426 (0.088)	0.43	0
Model 2	0.734 (0.110)	-0.034 (0.108)	0.058 (0.007)	0.183 (0.138)	16.440 (4.512)	0.418 (0.137)		-0.606 (0.156)	-0.426 (0.088)	0.28	0.84
Model 3	0.697 (0.112)	-0.098 (0.108)	0.058 (0.007)	0.179 (0.138)	16.137 (4.534)		-0.075 (0.026)	-0.578 (0.157)	-0.426 (0.088)	0.21	1.40

Parameter estimates that differ significantly from zero are shown in bold. The given PEs/SEs for 2-level factors indicate the difference between that level and the first factor level (non-Annex I in the case of A1; resident/short-distance migrant in the case of Mig; countries joining the EU before 2004 in the case of EU). Abbreviated variable names match those shown in Table 1. Primary habitat association did not feature in any of the selected models. In all model sets, the AIC_c weight of the null model was 0.

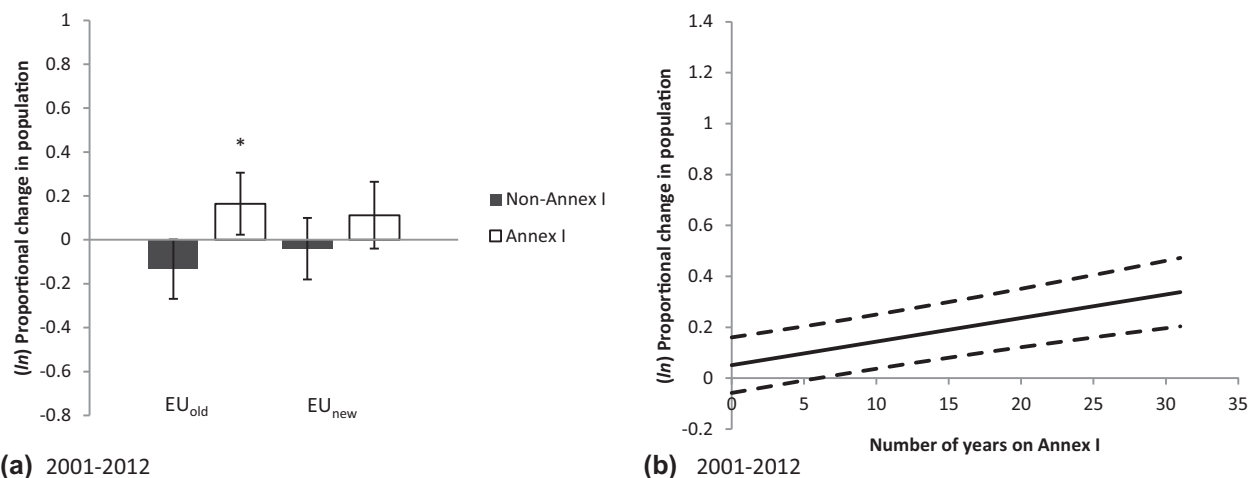


Figure 1 Difference from zero trend, 2001-2012, fitting Annex I status as a binary variable (a; asterisks indicating significant difference from zero trend); and the relationship between number of years a resident/short-distance migrant has been listed on Annex I (or the number of years that its country has been an EU Member State, whichever is lower) and population trend 2001-2012 (b; other explanatory variables held to mean or reference level), with 95% CI, derived from the best supported models in Table 2. EU_{old} countries joined the EU before 2004; EU_{new} from 2004 onward.

countries indicated that Annex I species had less positive trends in countries that acceded to the EU after 2003 (Table 2, Panel A), but these were still significantly more positive than those of non-Annex I species (Figure 1a).

Predictors of long-term (1980-2012) trends

The best supported models of long-term population trends again indicated a consistent positive effect of Annex I status, whether fitted as a covariate or as a binary factor (Table 2, Panels C and D; Figure 2b, c). They also indicated a significant additional effect of climate change suitability, indicating that species' long-term population trends have followed the trajectory predicted by their CST (Figure 2c). A negative effect of migration strategy was also retained in some of the best supported models, although the regression coefficients only differed significantly from zero in models that fitted Annex I status as a covariate. All models also included either generation length or clutch size and a positive effect of population size. All the best supported models also included an interaction between Annex I status and migration strategy, indicating that long-distance migrants on Annex I had trends that were less positive than those of other species on Annex I, although they did not differ significantly from zero, as was the case for non-Annex I migrants (Figure 2a). Again, a significant negative interaction between Annex I status when fitted as a binary variable and "old" and "new" EU countries indicated that Annex I species had less positive trends in countries that acceded to the EU more recently (Figure 2b).

Discussion

Over both time periods, species listed on Annex I of the Birds Directive had significantly more positive trends than species not listed on the Annex, and this effect was more pronounced in countries that had been in the EU for longer, although it was still present in the shorter time period in countries joining the EU since 2004 (which would have had to align their conservation legislation to the Birds Directive well before accession, lengthening the window over which the Birds Directive could potentially act). Annex I status was the most strongly supported correlate of population trend across all models, along with population size (Table 2). The positive impacts of the Directive on the trends of European birds between 1990 and 2000 (Donald *et al.* 2007) are therefore consistent over time and across a greatly expanded EU. The effect of population size may indicate that larger populations are more likely to be closer to the core of the species' range and therefore more robust to environmental change and are not comparable to the results of Inger *et al.* (2015) as we were not comparing trends of common and rare species.

An exception to the general pattern was the case of long-distance migrants, for which trends did not differ greatly between Annex I and non-Annex I species (Figure 2a). Long-distance migratory birds have been shown by a number of previous studies to be suffering population declines that might be due to changes on their African wintering grounds (Sanderson *et al.* 2006; Vickery *et al.* 2014). The reduced impact of Annex I listing on

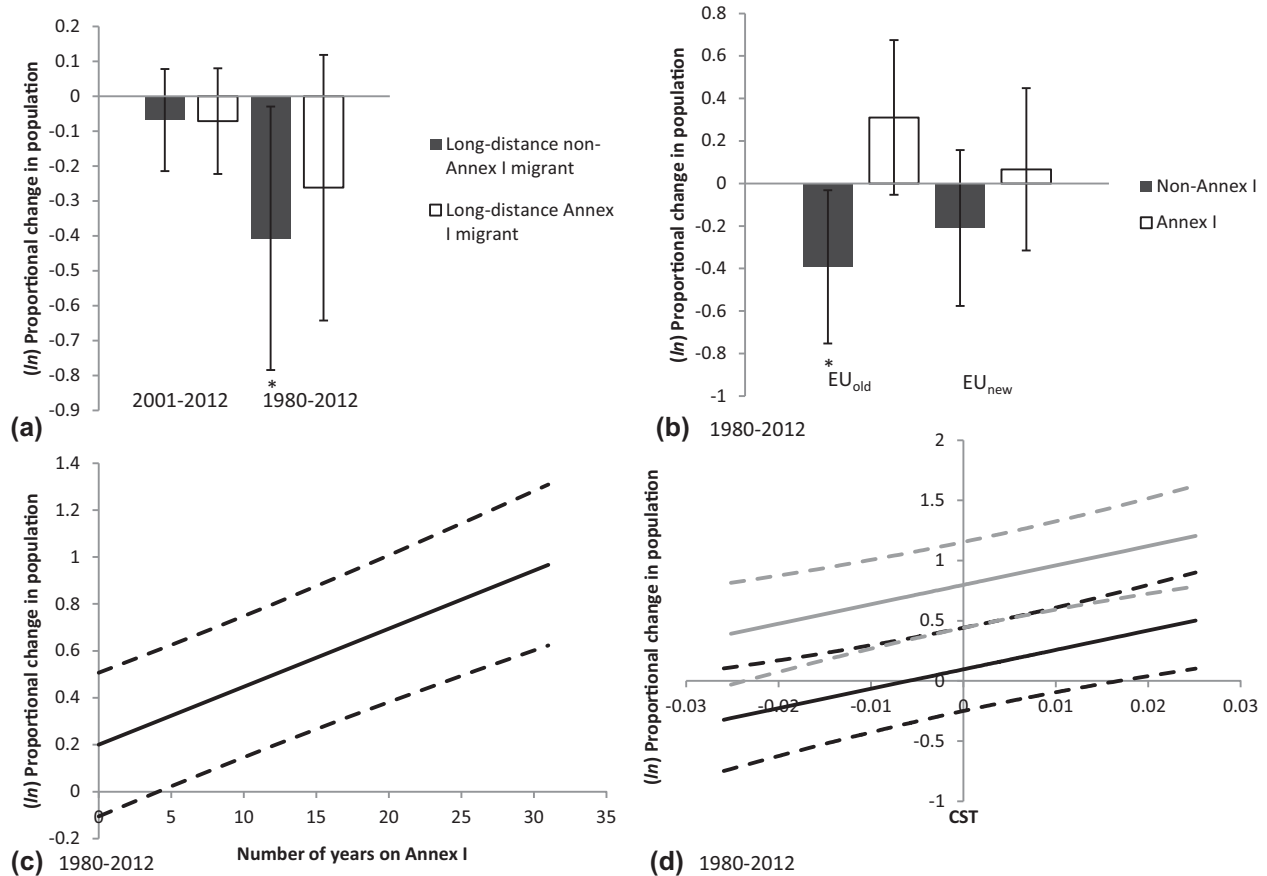


Figure 2 Differences from zero trend from the best supported model in each set fitting Annex I status as a binary variable for: (a) long-distance migrants; (b) “old” EU (which joined the EU before 2004) and “new” EU countries, with 95% CIs and asterisks indicating significant difference from zero trend; (c) the relationship between number of years a resident/short-distance migrant has been listed on Annex I (or the number of years that its country has been an EU Member State, whichever is lower) and population trend, with 95% CI, derived from the best supported model in Table 2, Panel C; and (d) the relationship between CST and population trend for Annex I (gray line) and non-Annex I (black line) residents/short-distance migrants, with 95% CI, derived from the best supported model in Table 2, Panel D, in both cases with other explanatory variables held to their mean or reference level.

these species might be expected if conservation investment in Europe were insufficient to offset increased pressures on migration or in the in African wintering areas. The short-term CST was probably based on too short a run of years to be expected to receive much support in the models of population trend, but the long-term CST was strongly supported in all model sets (Table 1, Panels C and D). This represents the most extensive (in terms of number of species, number of countries, and length of trend period) test to date of the response of European birds to climate change, and suggests that species are responding to climate change in the ways predicted by changes to their climate envelopes. Importantly, our results suggest that despite the clear responses of species to changing climate, Annex I status has a strong independent explanatory effect. Although climate change to date

has been moderate compared to that predicted to occur in the future, our results suggest that a changing climate does not undermine the effectiveness of mechanisms like the EU Birds Directive. Although the EU Birds and Habitats Directives do not explicitly mention climate change, they place legal obligations on EU Member States to take the measures necessary to facilitate the adaptation of biodiversity in Europe to climate change (Trouwborst 2011). However, adapting EU nature policy to climate change is likely to require substantial redistribution of resources (Lung *et al.* 2014).

We conclude that the long- and short-term trends of birds in an expanded EU show strong evidence of an effect of the EU Birds Directive that is additional to, and often greater than, that of other known drivers of population change, such as climate change, life history strategy,

and migration strategy. This is a rare demonstration of a positive impact of a multilateral conservation agreement, and suggests that such agreements can bring measurable benefits, even in an age of unprecedented climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Appendix S1: Criteria for recording of sub-species.

Appendix S2: Methods for imputing missing data.

Appendix S3: Multicollinearity between explanatory variables.

Appendix S4: Estimation of climate suitability trend.

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