

# Local human population increase in the non-breeding areas of long-distance migrant bird species is only weakly associated with their declines, even for synanthropic species

Will Cresswell<sup>1</sup>  | Nanchin Winifred Kazeh<sup>2</sup>  | Robert Patchett<sup>1</sup> 

<sup>1</sup>Centre for Biological Diversity, University of St Andrews, St Andrews, UK

<sup>2</sup>AP Leventis Ornithological Research Institute, Jos, Nigeria

## Correspondence

Will Cresswell, Centre for Biological Diversity, University of St Andrews, St Andrews, Fife KY16 9TH, UK.  
Email: wrlc@st-and.ac.uk

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## Abstract

**Aim:** To show how recent declines in populations of long-distance migrant birds are associated with recent increases in human population growth and agricultural intensification on their tropical non-breeding grounds, except for synanthropic species, where we expect the reverse.

**Location:** Breeding populations throughout Europe and North America spending the non-breeding season throughout Africa, and Central and South America, respectively.

**Methods:** We mapped 50 species of long-distance migrant birds from published tagging studies of 126 breeding populations and identified their breeding population trends from 2000 to 2015 from published Country or State census data. We then matched individual bird non-breeding locations, from each population, to local human population change and crop yield data. We used GLMs to predict whether bird population decline was associated with human population change or crop yield and whether this was dependent on if a species was synanthropic or not, controlling for absolute human population density, breeding and non-breeding location, migratory distance and phylogeny. We predicted that bird populations that spend the non-breeding season in areas of recent higher human population increase or agricultural intensification (crop yield) would show greater declines, but that declines would be less for species that frequently utilize anthropogenic habitats such as secondary woodland and farmland.

**Results:** Bird population change, even for synanthropic species, showed a significant negative relationship with relative human population change and crop yield (but this was weak, <2% and 6% of variance respectively), and this relationship was the same for the Neotropics and Africa, despite African human population change being three times larger.

**Main conclusions:** The results suggest that local human population change in the non-breeding area is likely to be only a relatively minor driver of migrant declines, and its effects may be through increases in agricultural intensification reducing carrying capacity, but we currently lack local studies to confirm this.

## KEYWORDS

agricultural intensification, anthropogenic effects, crop yield, migration, population declines

## 1 | INTRODUCTION

Migrant bird populations are declining globally, with major declines in both the Afro-Palaeartic (Sanderson, Donald, Pain, Burfield, & Bommel, 2006; Vickery et al., 2014) and Neotropical (Holmes, 2007; Robbins, Sauer, Greenberg, & Droege, 1989) regions. Declines in migrant birds have been linked with environmental change on the breeding and non-breeding grounds (Faaborg et al., 2010; Vickery et al., 2014). Habitat change on the non-breeding grounds can contribute to migrant declines (Newton, 2004) either directly through loss of suitable habitat reducing carrying capacity (e.g. Zwarts, Bijlsma, Kamp, & Wymenga, 2009) or reduction in habitat quality causing carry-over effects (e.g. Saino et al., 2004). Habitat change is often driven by increasing human populations (Ellis & Ramankutty, 2008; Foley et al., 2005; Gibbs et al., 2010) and high human population density and land use intensity results in lower species richness (Crist, Mora, & Engelman, 2017; Gagne, Sherman, Singh, & Meentemeyer, 2016; Pekin & Pijanowski, 2012). Human population growth is heterogeneous at a global scale (Ezeh, Bongaarts, & Mberu, 2012), varying between and within continents (Lutz & Samir, 2010).

Because human population growth is usually associated with land use change/intensification, which reduces carrying capacity for most species, we might then expect a negative relationship between human and migrant bird population change in the non-breeding area. It is important, however, to consider change in human population density rather than simply absolute human population density because we are interested in a dynamic process of how bird populations change and also because bird population trend data cover a wide range of starting populations that likely will have already been affected by human population density. Furthermore, because of this independence of bird population declines and absolute human population density we would predict, for example, that South and Central America, which have lower rates of absolute human population density than Africa (Lutz & Samir, 2010), show the same rate of bird population decline with human population increase as Africa.

Some migrant species, however, frequently use (Del Hoyo, Elliot, Sargatal, Christie, & Juana, 2018; Faaborg, 2002; Moreau, 1972) and can occur in relatively high density in human modified habitats (Johnson, Sherry, Holmes, & Marra, 2006; Jones, Vickery, Holt, & Cresswell, 1996; Karr, 1976; Wilson & Cresswell, 2006), and many migrants are generalist species able to spend the non-breeding season successfully in mid-successional and non-pristine habitats (Cresswell, 2014; Ivande & Cresswell, 2016). These synanthropic species (those that use human modified habitats such as secondary woodland and farmland) are likely to be less affected or even positively affected by human population change as more suitable habitat may be created. Consequently, we might predict slower rates of decline or even increases in populations of synanthropic bird species in non-breeding areas of high human population change. Alternatively,

agricultural habitats may not ultimately benefit synanthropic species, for example, because agricultural increases associated with human population change reduce carrying capacity through both reduced availability of original habitat and more intensively grown crops. Then, population trends of both synanthropic and non-synanthropic species may be negatively affected by human population growth. We might also expect indices of agricultural intensity, such as increasing average crop yield per unit area, to correlate negatively with bird population declines.

Here, we use accurate mapping (from tagging) of 50 species from 126 populations of long-distance migrants from North America and Europe that spend the non-breeding season in the Neotropics and Africa, respectively. We tested the hypotheses that:

1. migrant birds are declining more in non-breeding areas with greater rates of human population increase, regardless of absolute human population density, and so decline at the same rate in different regions.
2. increasing agricultural intensification is a driver of declines. If so, we would expect both synanthropic and non-synanthropic species to decline with both increasing human population density and increasing crop yield because carrying capacity is reduced in all habitats. If not, we would expect synanthropic species to show weaker declines or even increases where rate of human population increase is greater because synanthropic species would benefit from increased availability of suitable habitat, but still to show a negative correlation between bird population trend and crop yield.

## 2 | METHODS

### 2.1 | Migration data

We used the database in Patchett, Finch, and Cresswell (2018) that contained breeding and non-breeding locations for 909 individuals, from 126 populations of 50 species (see Table S1 and supplementary reference list for all studies used in analysis). Note sample sizes are larger in the study here because we used a wider range of sources of population trend estimates and the most recent data available, to reduce missing values. All data came from a comprehensive search of peer-reviewed tracking studies for all European and North American bird species classed (according to BirdLife; <http://www.birdlife.org/datazone/species/search>) as migratory land birds by entering the terms [latin name] AND migra\* AND (gps OR geolo\* OR satellite) into the Web of Science online library. From these studies, breeding and non-breeding (i.e. the site where an individual spent the majority of the non-breeding period after migration) locations of individual birds were extracted (or approximated from plotted map locations using Google Earth when precise coordinates were not given).

Our data are prone to two potential sources of error: imprecision in the translation of data from published figures to latitude–longitude coordinates via Google Earth (“translation error”), and inaccuracy of solar geolocator-derived positions in the original published data (“geolocator error”). Sensitivity analyses investigating whether these errors influence migratory connectivity measures and migratory spread were fully explored in Finch, Butler, Franco, and Cresswell (2017): translation and geolocator error were found to have a relatively small impact on these measures and were in all cases spatially unbiased and so are not considered further.

As in Finch et al. (2017), we restricted our study to the autumn (fall) migration of adult birds that were tagged on the breeding ground; we removed species with a sample size of one; we defined the Afro-Palaeartic system as populations breeding in Europe west of 65°E that have a non-breeding area in Africa south of 20°N; we defined the Neotropic system as all populations breeding in North America with a non-breeding area south of 30°N; and we classed birds tagged within 100 km of each other as coming from the same breeding population. Where there was more than one non-breeding site reported for an individual, we selected the non-breeding location where the individual spent the majority of the non-breeding period. If this information was unavailable, we selected the first reported non-breeding site. Of the 909 individual birds used for analysis, 41 were reported to have more than one non-breeding location after migration.

## 2.2 | Synanthropic species

All bird species were classified as either synanthropic or not on the basis of their non-breeding habitat use as described in the Handbook of Birds of the World Alive (Del Hoyo et al., 2018). Synanthropic species were ones that commonly use anthropogenic habitats when they are available: secondary woodland, plantations, farmland, urban or suburban areas; non-synanthropic species were ones that commonly use unmodified habitats: wetlands, primary forest or woodland or unfarmed savanna (Table S1). Twenty-two (44%) species were classified as synanthropic.

## 2.3 | Bird population data

We used bird breeding population trend data at the smallest spatial scale available from online and published sources. For the Afro-Palaeartic, this was usually at the country level and came initially from individual European countries contributing to the European Bird Census Council (EBCC) annual breeding bird monitoring schemes collated by the Pan-European Common Bird Monitoring scheme. The majority of data were obtained from the Status and Trends of Bird Populations (Article 12, Birds Directive 2009/147/EC) from the European Environment Agency (<https://www.eea.europa.eu/data-and-maps/data/article-12-database-birds-directive-2009-147-ec>). Significant annual rates of change were used where reported; where trends were not statistically significant, they were given a rate of 0. For non-EU countries or where data collated by

the European Environment Agency were missing or inconsistent, or more current and relevant (in terms of the period 2000–2015) analyses existed, individual country original source data were used. Annual percentage change for the North American region, US state or Canadian Province specific to the tagged species population for the period 2005–2015 was taken directly as reported from Sauer et al. (2017). The population trends used are given in Table S2, along with the sources of the estimates. Because of potential inconsistencies in methodologies between regions, we also simplified the bird population change into three broad categories (*increasing*, *stable* and *decreasing*) and repeated all analyses. A large outlier (Tawny Pipit with a single year's data of a very large annual decline) was identified, and this was excluded, but analyses are unaffected by its inclusion (Appendix S1). Analyses involving annual rates of change had a sample size of 124 populations because two populations only had trend data available.

## 2.4 | Human population and agricultural intensification data

Human population data were obtained from <http://www.worldpop.org.uk/>, using the 2000 and 2015 data sets for human population density for both Africa data (see Linard, Gilbert, Snow, Noor, & Tatem, 2012) and the Americas (see Sorichetta et al., 2015) at the 1 km square level. The mean population density per square kilometre was extracted at the geographic coordinate of the non-breeding location of each tagged bird averaged over a 100 km radius buffer using the raster package in R (R Development Core Team, 2014). These mean values were then averaged across all individuals in a population. The relative change in human population density was calculated by dividing the change in human population density between 2000 and 2015 by the 2000 human population density.

Human population data were temporally matched with the bird population change data as much as possible. On average, bird population data covered 10.8 years ( $\pm 0.25E$ ; range 1–15 years) of the human population change period (15 years, 2000–2015), with an average of 0.63 years' ( $\pm 0.135E$ ; range 0–5 years) data outside of this period (see Table S2).

An index of agricultural intensity (increasing crop yield) was obtained from published data on the sum of 5-year averages for 1995 and 2005 of yield for wheat, maize, rice and soybean (<http://www.earthstat.org/>; Monfreda, Ramankutty, & Foley, 2008; Ray, Ramankutty, Mueller, West, & Foley, 2012). The mean crop yield per square kilometre for each crop type was extracted at the geographic coordinate of the wintering location of each migrant averaged over a 100 km radius buffer (as above), and then, sum of the means for the four crop types was calculated. Note that this index is a measure of both increased proportion of land used for agriculture (many of the kilometre squares sampled at a buffered non-breeding location will have yields of 0 representing no agriculture in that square) and the intensity of any agriculture within a square where there is a crop yield recorded (higher yields in a square indicating more intensive farming on the agricultural land there). The derived crop yield index

for 2005 correlated positively and strongly with the relative change in human population density calculated above (Pearson's  $R = .66$ , adjusted  $R^2 = .44$ ). This strong relationship was driven by much lower values in the Neotropics compared with the Palearctic (Figure 2: correlation between crop yield index in 2005 and human population density change in the Neotropics had a Pearson's  $R = .29$  and an adjusted  $R^2 = .07$ , and in the Palearctic had a Pearson's  $R = .21$  and an adjusted  $R^2 = .03$ ). The relative change in crop yield was calculated by dividing the change in crop yield index between 1995 and 2005 by the 1995 crop yield index.

Other published potential indices of change in human impact on habitat for migratory birds did not provide temporally matched data for the bird population change (e.g. global human footprint in 1993 and 2009, <https://wchumanfootprint.org/>; Venter et al., 2016a, 2016b), but they correlated well with the population measures used for the mean non-breeding locations of the 123 bird populations sampled in this study (human footprint in 2009 with population index in 2015, Pearson's  $R = .73$ , adjusted  $R^2 = .53$ ; human footprint in 1993 with population index in 2000, Pearson's  $R = .78$ , adjusted  $R^2 = .61$ ).

## 2.5 | Statistical analysis

First, we used two GLMMs to explore the extent to which bird population annual rate of change or trend (*increasing*, *stable* and *decreasing* coded as 1, 0 and -1 respectively) depended on the rate of human population change:  $N = 124$  different populations or  $N = 123$  without the Tawny Pipit outlier, from  $N = 50$  or  $N = 49$  species respectively for annual change analyses;  $N = 126$ , from  $N = 50$  species for trend analyses (Table S1 and S2). We included fixed effects for the relative change in human population, the human population density in 2015, and the system (American or African flyway) and the interaction between the system and the relative change in human population. We also included the log of migration distance (great circle distance between breeding and non-breeding sites calculated using the `DISTHAVERSINE` function from the `geosphere` package in R), and breeding and wintering longitude and latitude, to control for potential confounding effects of location. We included a random effect of species nested within family nested within order to control for taxonomic biases and uneven sampling across species. Quadratic effects of change in human population density were not significant in any model tested.

Second, the same models were repeated but now including the variable synanthropic (1 or 0) as an interaction with rate of human population change to test whether the relationship between the rates of bird population change and human population increase depended on whether a species had an ecology that might benefit from increasing anthropogenic habitats.

Third, models were repeated exactly as with the first and second stages above but substituting in relative change in crop yield index 1995–2005 and crop yield index for 2005 (rescaled into an index approximately between 0 and 3) instead of human population change and human population density to test whether increases in

the intensity of agriculture predicted declines in bird populations. Quadratic effects of crop yield were not significant in any model tested.

The models were not confounded by spatial autocorrelation because the residuals of the final models were not correlated with the average nearest neighbour distance for the non-breeding locations (e.g. the main results model in Table 1A,  $F_{1,121} = 0.4$ ,  $p = .52$ ). There was also no relationship between absolute difference in bird population decline (range 0%–14.0%) for adjacent breeding areas and their distance apart (range 1.3–1,089.2 km apart), controlling for species in a mixed model ( $t = 0.2$ ,  $p = .81$ , 121 observations within 42 species). Populations of species and individuals were also sampled over a large spatial scale (Figure 1). Non-breeding populations sampled consisted of 2–119 individuals (mean  $18.1 \pm 3.5SE$  individuals) with a spread of 244–3,984 km ( $1,198 \pm 115SE$  km). Note that non-breeding spread of a population is significantly correlated with decline, but the direction of this relationship is positive in the American and negative in the African system (Patchett et al., 2018). Therefore, if variation in non-breeding spread (i.e. a proxy of degree of spatial independence of points) is confounding the relationship between bird population change and human population change (e.g. small spread species occurring more often in low human population change areas) then we would not expect the same relationship between bird and human population change across systems. There was, however, no significant interaction observed between human population change and system (see below).

All models were fitted with a Gaussian distribution and an identity link function using the `NLME` package in R. Model fit was assessed by visual inspection of residuals plotted against fitted values and quantile plots and were reasonable in all cases after log-transforming migration distance. Predicted values were plotted using the `LME4`, `AICCMODAVG` and `GGPLOT2` packages in R; variance was partitioned into main and random effects in mixed models using `MUMIN`.

## 2.6 | Sample size and bias

The unit of statistical analysis is population but controlling for repeated samples within species and higher levels of taxonomic order that might affect independence. Mean values were calculated from individual tracked birds in each population. Many of these samples within populations are small: 54 (44%) of populations comprise of 2, 3 and 4 individuals tracked. Restricting analyses to populations with larger and more representative samples unreasonably reduces overall sample size. Removing small sample size populations will also bias against finding any relationship between human population change on the non-breeding ground and bird population change.

First, to effectively test whether there is any relationship between non-breeding location and human population change we need variation in human population change there and removing populations with small sample sizes homogenises mean human population change. As sample size increases, so the non-breeding migratory spread increases substantially (adj.  $R^2 = .44$ ; see Finch et al., 2017, Figure S1), with an asymptote of the order of 3,500 km (i.e. a

continental scale). Sampling populations over increasingly large and so overlapping non-breeding ranges will therefore lead to increasingly similar human population change estimates. Similarly, weighting of regressions by sample size would also exaggerate the effects of populations homogenized for human population change. But, if we use sample size/maximum non-breeding spread we then weight those populations that have the highest sample size relative to the non-breeding spread: those populations with a disproportionately larger sample size for their migratory spread are likely to be more representatively sampled. Weighting in this way has only little or no biological or statistical affects (Table S3).

A second, and perhaps more important, biological problem is that populations that spend the non-breeding season in areas of high human population change are likely to be declining and so will be more likely to have lower survival between breeding seasons. Populations tagged from breeding areas with higher non-breeding survival will have greater recovery rates and so larger sample sizes. Most geolocator studies already have very small sample sizes, and low overwinter survival often reduces sample size down to very low numbers. Therefore, excluding those with the lowest sample sizes will likely exclude those populations that encounter the

greatest rates of human population change on the non-breeding ground.

### 3 | RESULTS

#### 3.1 | Hypothesis 1: Migrant birds are declining more in non-breeding areas with greater rates of human population increase

As predicted, relative human population change in the non-breeding area was significantly negatively correlated with bird population change (Table 1A; Figure 1a). Bird population declines were significantly greater in the Neotropics for any given level of human population change (Table 1A; Figure 1a). Fixed effects accounted for 14% of variance and random effects 31%; <2% of variance was accounted for by relative human population change. The results were broadly similar when considering bird population trends rather than annual rate of bird population change (Figure S1) although the result with respect to bird population declines being significantly greater in the Neotropics for any given level of human population change was not then significant.

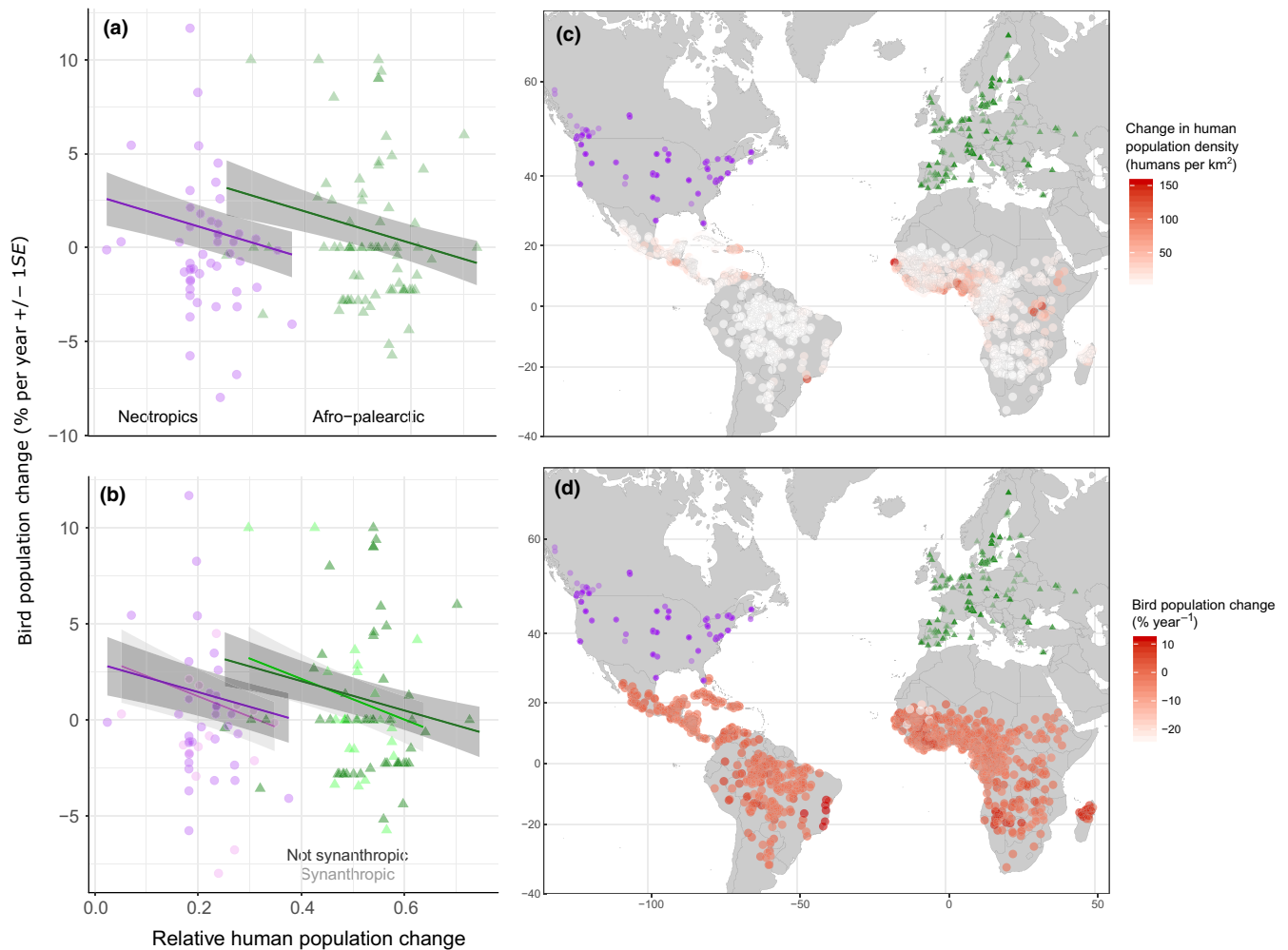
**TABLE 1** Results of mixed model analyses to test whether bird population decline was dependent on (A) rates of human population change or (B) crop yield

	Estimate	SE	df	t value	p value
<b>A</b>					
(Intercept)	0.23	18.4	100.0	0.013	.99
Human population change	-8.4	3.8	113.0	-2.195	<b>.030</b>
Nearctic system <sup>a</sup>	-10.3	3.1	103.2	-3.284	<b>.0014</b>
Human population 2015	0.0092	0.0075	106.8	1.228	.22
log(Migration Distance)	1.6	2.5	102.6	0.632	.53
Breeding longitude	-0.0703	0.022	111.5	-3.128	<b>.0022</b>
Breeding Latitude	-0.16	0.079	110.8	-2.074	.04
Wintering Longitude	0.0075	0.030	112.1	0.252	.80
Wintering Latitude	0.021	0.067	79.8	0.311	.76
<b>B</b>					
(Intercept)	15.1	19.2	103.7	0.8	.43
Crop yield change	0.87	0.98	110.4	0.9	.36
Nearctic system <sup>a</sup>	-9.0	3.0	107.06	-2.9	<b>.0035</b>
Crop yield 2005	-1.3	0.58	83.3	-2.2	<b>.031</b>
log(Migration Distance)	-0.88	2.6	103.7	-0.3	.73
Breeding longitude	-0.080	0.023	112.6	-3.5	<b>.0007</b>
Breeding Latitude	-0.094	0.080	108.4	-1.2	.24
Wintering Longitude	0.018	0.030	112.1	0.6	.57
Wintering Latitude	-0.037	0.069	89.9	-0.5	.60

Note: Both models included random effect of Order/Family/Species; N = 123 populations, 49 species, without the outlier Tawny Pipit.

<sup>a</sup>Intercept set to the Afro-Palaeartic system.

Statistically significant parameters have their P values in bold.



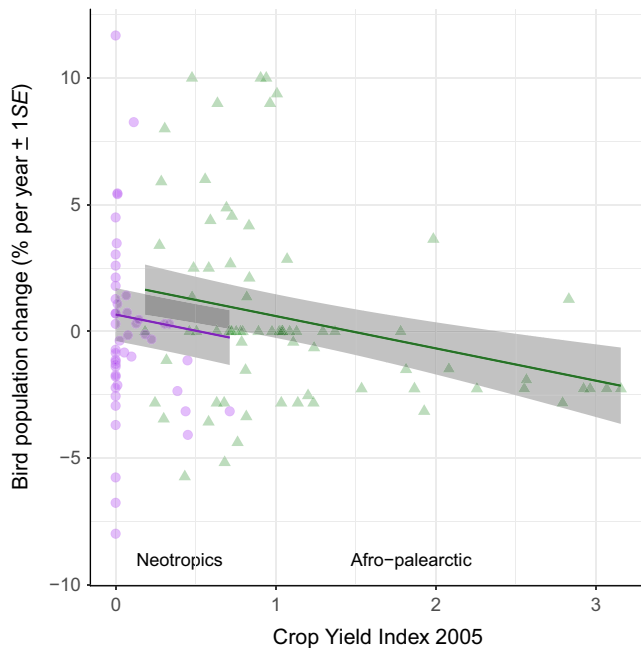
**FIGURE 1** (a) Predicted values from the model testing how annual percentage change in bird population size was dependent on relative human population change (see Table 1A). (b) Predicted values from the same model but with the inclusion of the interaction between species that do (synanthropic), or do not, favour anthropogenic habitats and relative human population change. The relationship between bird population change and human population change is significant and very similar for both systems, but for any given level of human population change, bird population trends are more significantly negative in the Neotropics; average bird population change was very similar for synanthropic and non-synanthropic species (i.e. predicted lines for synanthropic species lie more or less directly behind those of non-synanthropic species). (c) Change in absolute human population density (2000–2015): human population density per square kilometre was averaged over a 100 km circular buffer around each non-breeding location, and then, the average of these values calculated for all non-breeding locations for a population. (d) Annual change in bird population (mostly over the period 2000–2015), for each non-breeding location; breeding locations of the populations sampled are plotted as green triangles or purple circles

As predicted, there was no significant difference in the negative gradient of the relationship between relative human population change and bird population change between the Neotropics and Afro-Palaearctic systems (interaction between system\*relative human population change added into the model in Table 1A:  $-7.3 \pm 8.7$ ,  $t_{108,1} = -0.8$ ,  $p = .41$ ), although the model was improved by including the interaction (delta AIC =  $-4.9$ ) suggesting that bird declines in response to human population change may have been steeper in the Neotropics. The effect of human population density in 2015 was non-significant ( $0.011 \pm 0.0078$ ,  $t_{106,4} = 1.4$ ,  $p = .16$ ). Other terms in the model also did not have statistically significant effects, apart from a significant negative correlation between both breeding longitude or latitude and population change, with more easterly breeding populations in both systems having more negative population trends ( $-0.069 \pm 0.023$ ,

$t_{110,0} = -3.1$ ,  $p = .0028$ ) and more northerly latitudes having more negative population trends ( $-0.17 \pm 0.079$ ,  $t_{109,3} = -2.2$ ,  $p = .033$ ). The results were broadly similar when considering bird population trends rather than annual rate of bird population change (Figure S1) although the results with respect to breeding longitude and breeding latitude were not then significant. The results were very similar when including the Tawny Pipit outlier (Figure S3).

### 3.2 | Hypothesis 2: Synanthropic species show weaker declines unless declines are driven by agricultural intensification

Against prediction, synanthropic species showed no evidence that they were affected by human population change differently to



**FIGURE 2** Predicted values from the model testing how annual percentage change in bird population size was dependent on crop yield in 2005, as the best available index of agricultural intensification (see Table 1B). The relationship between bird population trend and crop yield is significant

non-synanthropic species. Synanthropic species showed a weak steeper decline with relative population change when included in the model (in Table 1A), and the model was slightly improved by including the interaction (delta AIC =  $-3.2$ ), although the interaction term was not significant ( $-3.0 \pm 4.2$ ,  $t_{96.9} = -0.7$ ,  $p = .49$ ): Figure 1b. If the interaction is removed, synanthropic species show no difference in population trends compared with non-synanthropic species ( $-0.73 \pm 0.67$ ,  $t_{82.4} = -1.1$ ,  $p = .28$ ), and the original model (in Table 1A) was barely improved (delta AIC =  $-0.2$ ). All other variables had similar biological and statistical effects to when synanthropic was not included in the model (i.e. the model in Table 1A): relative human population change remained significantly negatively correlated with bird population trend ( $-8.1 \pm 3.8$ ,  $t_{112.1} = -2.1$ ,  $p = .038$ ). The results are broadly similar when considering bird population trends rather than annual rate of bird population change (Figure S2) although the results with respect to breeding longitude and breeding latitude were not then significant. The results were very similar when including the outlier from Tawny Pipit (Figure S4).

Change in crop yield index was not correlated with bird population change, but absolute crop yield index (for 2005) in the non-breeding area was significantly negatively correlated with bird population change (Table 1B; Figure 2). Fixed effects accounted for 18% of variance and random effects 40%; 6% of variance was accounted for by crop yield index. Substituting crop yield 2005 into the main human population change model (Table 1A) for human population change and population density in 2015 (which correlate well with crop yield, see Section 2) resulted in a better model (Table 1B:

delta AIC =  $-4.7$ ). Synanthropic species showed a less negative decline with crop yield index when the interaction was included in the model (in Table 1B), although this was not significant ( $0.35 \pm 0.98$ ,  $t_{103.5} = 0.4$ ,  $p = .71$ ). The interaction between change in crop yield and synanthropic species was also not significant when included in this model ( $-1.4 \pm 2.1$ ,  $t_{89.7} = -0.7$ ,  $p = .50$ ). If the interactions are removed, synanthropic species show no difference in population trends compared with non-synanthropic species ( $-0.75 \pm 0.66$ ,  $t_{83.6} = -1.1$ ,  $p = .26$ ). All other variables had similar biological and statistical effects to when synanthropic was not included in the model (i.e. the model in Table 1B): crop yield remained significantly negatively correlated with bird population trend ( $-1.2 \pm 0.58$ ,  $t_{79.9} = -2.1$ ,  $p = .038$ ). The results were broadly similar when including the outlier Tawny Pipit (Figure S5) or when considering bird population trends rather than annual rate of bird population change (Figure S6) although the relationship between crop yield index and bird population trend was only marginally statistically significant.

## 4 | DISCUSSION

Migrant bird populations showed a significant negative relationship with relative human population change or crop yield (as an index of increasing agricultural intensity), and this relationship was the same for the Neotropics and Africa, despite rates of human population change being about three times larger on average in Africa. These results were as expected: as human populations increase, habitat availability and carrying capacity for many animal species reduces (Foley et al., 2005; Gibbs et al., 2010; Yom-Tov, Hatzofe, & Geffen, 2012). Despite the obviousness of this main result, which emerges from most conservation studies, there are two aspects of this result that are novel and of great interest. The first is that the amount of variance in bird population declines accounted for by human population change on the non-breeding ground is relatively small, and the second is that whether or not a species favours anthropogenic habitats apparently makes little difference. Therefore, this study suggests for the first time that habitat quality for migrant birds generally on the non-breeding ground might be important rather than just its availability. However, neither habitat availability or quality are likely to be the main drivers of migrant population declines in two of the four global migrant bird flyways.

Before discussing the results in detail, it is very important to point out the limitations in the data. Many (44%) of populations sampled have only 2, 3 or 4 mapped locations, and so these populations may not be representative of the average human population change over the whole non-breeding range. The results of this study depend crucially on including all the data (although populations with only one mapped non-breeding location were excluded from the onset to reduce this). Populations with small sample size may, however, have a greater biological significance because they represent populations where non-breeding survival may be lower (see Section 2), although this may arise because of mortality occurring during migration rather

than on the non-breeding ground. If this is the case, including small sample size populations should simply increase the noise in the data, weakening any correlations, and we would conclude correctly that human population change operating on the non-breeding ground was relatively unimportant. But, the issue of whether including small sample size studies increases meaningful variation in human population change is less clear. As above, there may be too few locations to accurately represent range and so the human population change affecting a breeding bird population: smaller ranges result from smaller sample sizes (Finch et al., 2017). This may then result in more distinct values of human population change because a smaller range means less regression to the mean values of human population change across very large (continent scale) ranges. A greater range of variation in human population change rate arose from including small sample size populations, and the results of this study depend on this. But, this is unlikely to have led to a biased stronger result that would over-represent the strength of the negative relationship between human population change and bird population change, because small range and small sample size populations tend to be relatively more common at both low and high values of human population change (see Figure S7). And, if this was not meaningful variation overall, we would then not expect any correlation between human and bird population change—it would simply add random noise at either end of the distribution of human population change. Populations with small sample sizes may also have greater biological significance in the analysis if geolocator studies have targeted bird species to investigate declines specifically linked to conditions on the non-breeding ground, but to our knowledge, the Aquatic Warbler *Acrocephalus paludicola* is the only species included in our analysis that might (arguably) fit this criterion. Small sample size populations are in any case evenly distributed across the full range of bird population trends, both positive and negative (see Figure S7). But, the current availability of data does not allow for conclusive control of these confounding effects.

We show that the relationship between migrant bird population declines and human population increases on their non-breeding grounds only accounts for a small part of the variation in migrant bird population declines (<2%). Most variation in declines was accounted for by species identity (and therefore likely ecology): most declines have very species-specific causes (Hagan & Johnston, 1992; Vickery et al., 2014). Habitat and climate change is likely to limit populations for many migrant species more on the breeding grounds or during migration (Newton, 2004), so that the reduced carrying capacity on the non-breeding grounds makes relatively little difference.

It is important to note, however, that weak correlations are likely to arise methodologically because of the scale differences involved in monitoring breeding and non-breeding populations (Cresswell, 2014). Bet-hedging strategies (e.g. see Reilly & Reilly, 2009) that result in a wide spread of juveniles across the non-breeding ground make populations susceptible to any habitat changes that occur over a wide area (Finch et al., 2017). But, these effects will be diluted because only some of the population will be

in the non-breeding areas affected. In contrast, any habitat or climate change operating on the breeding ground is likely to affect a greater proportion of individuals in the breeding population being monitored. As the geographic range of the breeding population considered increases, so the proportion of individuals in the breeding population affected by any local detrimental changes in non-breeding conditions increases, and so strong correlations between non-breeding conditions and breeding population change may arise (e.g. Baillie & Peach, 1992; Thingstad, Nyhoim, & Fieldheim, 2006). Furthermore, in this analysis we have taken bird population data on the scale of single European countries and North American states or Provinces, whereas the correlated human population change data come in most cases from averaging across a much larger non-breeding range encompassing several countries or continental regions (Finch et al., 2017). The consequence of both effects will be to reduce the strength of correlations between conditions at non-breeding locations with breeding population trends. Ideally, we should compare the population trends for separate breeding populations that visit separate non-breeding areas with distinct environmental conditions, at the same scale, to identify non-breeding drivers of population change, but unfortunately low connectivity in most species precludes this. This is, however, one of the main points of this study: to empirically confirm the weak effect of non-breeding conditions on population trends of migrant birds generally because of low connectivity.

The mechanism for the weak relationship between change in human population density and bird population declines we observe is likely to be transformation of habitat into agricultural land and then intensification of agriculture in the transformed habitats: this was captured by our measure of crop yield. Agricultural expansion and intensification are usually linked to human population increase (Laurance, Sayer, & Cassman, 2014), but globalization and urbanization may decouple this (e.g. Lapola et al., 2014). A stronger relationship was established between bird population declines and a direct measure of agricultural intensification (crop yield) than with human population change. The two measures were well correlated in this study, but the difference may suggest that intensification of agriculture on existing agricultural land rather than simply habitat change is also important for migrant birds. This is also supported by the result that synanthropic species showed no significant difference in their rates of decline compared with non-synanthropic species, so even if increasing human population in an area creates more habitat for some species, that habitat is likely to be of poor quality. But, our use of the crop yield index here cannot distinguish well between increased amount of land converted to agriculture from increases in intensity of agriculture on any existing agricultural land. Either or both may lead to declines in populations of migrants, and it is possible that the former may apply more strongly in Africa and the latter more strongly in the Neotropics where human population change and so land use change is less. It is also important to note that low values of crop yield index resulted in quite variable population trends (see Figure 2), suggesting that absence of agricultural intensification



does not guarantee stable or increasing bird populations and that human population increase likely impacts on bird populations in the non-breeding area through mechanisms other than agriculture. It is also noteworthy that change in crop yield was not a predictor of bird population declines, and only absolute crop yield index was a predictor. This may have been because the time period of the best available crop yield data was not well matched with the bird population trend data, or because there was relatively little change in intensity between 1995 and 2005.

We found the relationship between change in human population density or crop yield and bird population density to be *steeper* for synanthropic species (although the difference was not significant). Even with changes to the classification of what entails synanthropic species, there would unlikely be a strong signal emerging of the importance of use of secondary or anthropogenic habitats in the non-breeding season in overall migrant bird population trends. Nevertheless, some species may be benefitting from increased availability of non-breeding habitat, for example Northern Wheatears *Oenanthe oenanthe* (Wilson & Cresswell, 2010) and Bobolinks *Dolichonyx oryzivorus* (Renfrew, Hill, Kim, Romanek, & Perlut, 2017) that use intensively farmed habitat, however, this is not occurring in sufficient numbers of populations or strongly enough to change the general relationship between human population increase and migrant bird population decline (see Table S2).

The results confirm human population change in the non-breeding area is likely to be a driver of migrant declines (albeit a relatively minor one), but more importantly they suggest that this is regardless of whether a species can use anthropogenic habitats or not. Agricultural expansion and intensification may then be a mechanism for the migrant bird declines (Frenzel, Everaars, & Schweiger, 2016): increasing human populations reduce the carrying capacity of any habitat because increasing land for agriculture and increasing agricultural output on that land leaves little room for other species (Gaston, Blackburn, & Goldewijk, 2003; Henderson, Fuller, Conway, & Gough, 2004; Reif, 2013). Carrying capacity for non-synanthropic species is likely reduced through habitat loss and carrying capacity for synanthropic species is reduced through reduction in habitat quality. The situation we observe in this study in developing southern countries possibly then parallels what happened to European and North American resident bird populations during the agricultural intensifications that reduced carrying capacity there in the last century (Chamberlain, Fuller, Bunce, Duckworth, & Shrubbs, 2000; Donald, Green, & Heath, 2001; Stanton, Morrissey, & Clark, 2018). We only systematically monitor—and this is particularly true in the Afro-Palaearctic system (although see Wotton et al., 2017)—bird populations in northern temperate areas. Therefore, the only Afrotropical or Neotropical species we monitor effectively are those species that migrate to breed in these northern temperate areas. This study may then be simply picking up the effect of agricultural expansion and intensification on bird populations generally—both residents and migrants—in Africa and the Neotropics. Many migrant species are

low connectivity, high spread (Finch et al., 2017), generalist species, which occur in anthropogenically modified habitats and that do better when these habitats are used less intensively, for example, land-sharing (see Green, Cornell, Scharlemann, & Balmford, 2005). But, managing farmland for biodiversity is not a major conservation priority on the breeding, non-breeding or staging areas, because of universal agricultural intensification to feed increasing human populations (Brown, Llewellyn, & Nuberg, 2018; Donald, Sanderson, Burfield, & Bommel, 2006; Gamero et al., 2017). Consequently, it is perhaps not unexpected that most migrant species are declining.

But, the most important result of this study is that local human population change in tropical non-breeding areas may be relatively minor factor in influencing migrant population dynamics: conservation management of staging areas and the breeding areas may have the most effect (although only on average, and, of course, not all species will fit this general pattern). It is important to note, as above, that the quality of the data is relatively poor and this may prevent the detection of a stronger relationship if it exists. Also, human population density and crop yield are only two possible proxies for anthropogenic effects (although many of these measures, such as they exist on the spatial scale considered here, correlate well with them): other unconsidered factors are likely to also affect bird populations on the non-breeding ground. And, because of the effect of low connectivity diluting the effects of local non-breeding area habitat change for any breeding population, even if we do identify predictors, their effect on a specific breeding population may seem to be relatively small (Cresswell, 2014).

But, conservation measures will always be necessary in the non-breeding areas, even if they are not *the priority* (e.g. Morrison, Robinson, Butler, Clark, & Gill, 2016), for long-distance migrant birds. Migrant birds clearly require some reasonable quality habitat to be available in the non-breeding area, even if their populations are currently *mostly* limited elsewhere. And, habitat change and agricultural intensification in tropical areas must also be affecting local bird populations strongly (Newbold et al., 2015). But, there are almost no empirical field studies in Africa (Adams, Small, & Vickery, 2014; Wotton et al., 2017), and relatively few in the Neotropics (e.g. Di Giacomo & de Casenave, 2010; Frutos, Reales, Lorenzon, & Ronchi-Virgolini, 2016; Shaver et al., 2015), that monitor bird populations in agricultural habitats. Clearly, we need further research into how biodiversity is maintained, and how migrants survive, on agricultural land (e.g. land-sharing solutions) in tropical areas and particularly Africa, where even local baseline biodiversity monitoring is lacking (Cresswell, 2018).

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## ORCID

Will Cresswell  <https://orcid.org/0000-0002-4684-7624>

Nanchin Winifred Kazeh  <https://orcid.org/0000-0002-2980-9650>

Robert Patchett  <https://orcid.org/0000-0003-4105-3136>

## DATA AVAILABILITY STATEMENT

All data were collected from sources freely available in the public domain; final databases and R scripts have been archived in Dryad <https://doi.org/10.5061/dryad.n2z34tms1>.

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**BIOSKETCHES**

**Will Cresswell** is a Professor of Biology at St Andrews University, Scotland, researching the factors determining the density and distribution of migrant birds, particularly in Africa, to determine why they are almost universally declining.

**Robert Patchett** is a PhD student at St Andrews researching the ontogeny of migration routes and non-breeding site selection.

**Nanchin Winifred Kazeh** is a Masters graduate and research associate at the AP Leventis Ornithological Research Institute with responsibility for data management of the ongoing Nigerian Bird Atlas programme.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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