Phenology and climate change in Africa and the decline of Afro-Palearctic migratory bird populations

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Abstract

The populations of many Afro-Palearctic migratory bird species have declined over the last 50 years, for reasons that remain poorly understood, but which could include major environmental changes in Africa. We mapped, for the first time, the aggregated population trends of migratory species onto their non-breeding distributions in sub-Saharan Africa and used regression models that account for non-stationarity to examine correlations between assemblage population trend indices and changes in climate and vegetation phenology over the same time period. This also allowed us to map geographical variation in these relationships across Africa. Our results revealed that relationships between population trends of migrant bird species and climate and phenology are spatially highly variable, and that there are no consistent, flyway-wide associations between climate or phenology and population trends. However, we found evidence that migrant population changes may be more closely linked to indices of vegetation senescence and climate than to indices of greening, suggesting further lines of investigation. Simply using cumulative Normalised Difference Vegetation Index (NDVI) across Africa greatly underestimates the extent to which phenology and climate vary spatially, as do the relationships between population trends and these environmental variables. Furthermore, much better data on the nonbreeding ecology and distributions of migrants, including connectivity between breeding and wintering grounds, are needed if we are to assess with any confidence the extent to which they may be impacted by changes in environmental conditions in Africa. Until then, we suggest that there is no simple relationship between migrant populations and NDVI across species’ ranges, and that further studies should, at the very least, consider the multiple dimensions of phenology and the potential for spatial variation in relationships.

Introduction

Populations of many Afro-Palearctic migratory bird species have declined over the last 50 years, these declines being greater than in resident species or short-distance migrants (Sanderson et al. 2006, 2016; Vickery et al. 2014). The drivers of these declines are not well understood. The complex annual cycle of migrants means that they are vulnerable to factors acting on their breeding, wintering and/or staging grounds (Newton 2004). Detrimental changes in conditions at any of these locations could have a negative impact on their survival or productivity, ultimately causing population-level declines if the changes are sufficiently severe and/or persistent (Pearce-Higgins et al. 2015). Confounding factors, interactions between drivers and our lack of knowledge of the
migratory routes, wintering ranges and non-breeding habitat preferences of many species, make the contribution of individual drivers difficult to determine.

Many studies have focused on factors that might affect Afro-Palearctic migrants on their breeding grounds, perhaps reflecting the availability of data and the greater resources for research in Europe compared to Africa, rather than an indication that factors on the breeding grounds are necessarily more important (Adams et al. 2014; Vickery et al. 2014). A review by Vickery et al. (2014) concluded that in breeding areas, degradation of habitats impacted the largest number of species, while in non-breeding areas the interacting factors of climate and anthropogenic habitat degradation appeared to be the most important. Of the non-breeding season factors investigated, human-related habitat change was reported as by far the most frequently significant variable, with 89% of studies suggesting negative effects on birds (Vickery et al. 2014).

The East Atlantic flyway links breeding grounds in arctic and temperate regions of western and central Europe with non-breeding areas in temperate and tropical regions of western and southern Africa (BirdLife International 2010). Anthropogenic modifications to the natural environment are evident throughout the East Atlantic flyway. In recent decades, high rates of environmental change have occurred in sub-Saharan Africa, where there is increasing pressure on land to provide food and other resources for a rapidly growing human population (Venter et al. 2016; Cotillon et al. 2014). This has led to loss of trees in wooded savannah, linked to clearance for agriculture, fuel wood and grazing (Brink and Eva 2009; Ockendon et al. 2012), and loss of wetland habitats, linked to water extraction for irrigation and construction of dams for hydro power (Adams et al. 2014). There have also been significant levels of agricultural intensification, including increased grazing, expansion of cultivated land at the expense of natural habitats, and increased use of fertilizers and pesticides (Morrison et al. 2013; Adams et al. 2014; Atkinson et al. 2014; Vittek et al. 2014).

Atkinson et al. (2014) suggested that Afro-Palearctic migrants dependent on dry open habitats (dry farmland and grassland) declined most between 1970 and 1990, whereas species associated with more moist, vertically structured habitats (tree and shrub rich farmland) and grassland declined most between 1990 and 2000. This suggests that it is important to take account of species’ habitat associations when looking at patterns of population change. It also indicates that the drivers of change may vary between species associated with different habitats.

Changes in land use or land cover are not uniform across Africa (e.g. Brink and Eva 2009). They arise from the interaction of local decisions by farmers and other land managers, with the context set by national policies and international investment, aid and trade (Atkinson et al. 2014). This leads to complex spatial patterns of change that are very difficult to measure at a continental scale (Adams et al. 2014). Concurrently, environmental conditions and patterns of weather and climate have also changed, both through natural fluctuations and as an indirect effect of anthropogenic activities and greenhouse gas emissions. Numerous studies have demonstrated a link between climatic conditions on passage and wintering grounds, especially precipitation, and adult survival (Peach et al. 1991; Baille and Peach 1992; Szep 1995; Nevoux et al. 2008; Robinson et al. 2008; Norman and Peach 2013; Ockendon et al. 2014; although see Masoero et al. 2016) and the reproductive success (Zwarts et al. 2009; Finch et al. 2014) of migratory species, as well as the timing of migration (Robson and Barriocanal 2011).

The use of satellite remote sensing data can help to address the challenge of measuring and monitoring largescale changes in land cover (a surrogate for habitat), and allows assessments to be made over large geographical areas and timescales. While not all features of habitats can be detected by satellite remote sensing, it is possible to capture information about photosynthetic activity, and therefore vegetation and vegetation growth. A remotely sensed variable that is often used as a proxy for vegetation or habitat quality is the Normalised Difference Vegetation Index (NDVI). NDVI is related to photosynthetic activity and provides a relative measure of primary productivity.

Several studies have investigated links between NDVI on the wintering grounds of migratory birds and the timing of spring migration (Saino et al. 2004a; Gordo and Sanz 2008; Tøttrup et al. 2008; Balbontin et al. 2009; Robson and Barriocanal 2011), timing of breeding (Saino et al. 2004b; Visser et al. 2015), clutch size (Saino et al. 2004b) and population trends (Ockendon et al. 2014), with mixed results. For example, Ockendon et al. (2014) found that of the 16 Afro-Palearctic migrant bird species they investigated, NDVI had a significant correlation with population growth rates in just four.

Almost all these studies implicitly assume a straightforward relationship between population and NDVI, with higher values of NDVI indicating more mesic and hence more favourable environmental conditions for species. However, NDVI varies not only with environmental conditions but also with land use and habitat type. For instance, NDVI in well-vegetated areas such as forest is much higher than sparsely vegetated scrub areas. These differences can be used to map land cover (e.g. Mayaux et al. 2004). Rapid changes in NDVI profile can therefore be used as an indicator of land cover or land use change.
In addition, vegetation phenology, that is, the timing of growing seasons, may play an important role in determining habitat quality for migrants at specific times of year. The life-history strategy of migratory species means that they may be particularly susceptible to the effects of phenological mismatch, especially if differential changes in phenology occur on their breeding and wintering grounds (Emmerernegger et al. 2016). Migration is energetically expensive and requires sufficient food availability both prior to departure and on arrival. Thus, even if the magnitude of resources remains the same, changes in the timing of availability with changing land management practices, habitat degradation or climate could result in birds departing for migration in poorer condition, or arriving too early or too late with respect to environmental conditions or the availability of resources at their destination.

There is already evidence that climatic and phenological change in Europe is a factor in population declines in migratory birds (Both et al. 2006; Samplonius et al. 2016). Optimal timing of reproduction has been advancing in the northern hemisphere as a result of climate change, and long-distance migrants now arrive later relative to spring temperatures than previously (Møller et al. 2008; Saino et al. 2011). This can result in reduced reproductive success (Saino et al. 2017) and might give resident species, which are better able to adapt to changing conditions on breeding grounds, a competitive advantage (Wittwer et al. 2015).

Although studies have revealed the potential impact of climatic and phenological change on the breeding grounds, little attention has been given to African vegetation phenology and the impact it could have on migrant bird populations during the non-breeding season (although see Emmerernegger et al. 2016). We use a dataset on global vegetation phenology to characterize long-term trends in the lengths and timing of growing seasons, as well as rates of vegetation greening and senescence, across sub-Saharan Africa. We then use geographically weighted regression (GWR) to examine correlations between changes in climate, phenology and the population trends of migratory species across their non-breeding ranges. GWR not only allows us to identify environmental trends that may be associated with population declines beyond simple measures of cumulative NDVI but also to map geographical variation in relationships across Africa.

Materials and Methods

Species selection

Maps of species’ breeding and non-breeding distributions (BirdLife International 2016) were used to select all passerines and near-passersines with a breeding range overlapping Europe and the East Atlantic flyway and a non-breeding range overlapping sub-Saharan Africa and the East Atlantic flyway, giving a total of 72 species (Table S1). We used the geographic definitions of Europe from the European Red List of Birds (BirdLife International 2015), the East Atlantic flyway from BirdLife International (2010) and defined sub-Saharan Africa as the Afrotropical biome based on Olson et al. (2001).

Habitat assemblages

Data on each species’ non-breeding habitat associations were extracted from BirdLife’s datasets (BirdLife International 2016). We included all level 1 habitat associations listed as ‘major’ or ‘suitable’, but excluded those listed as ‘marginal’. This gave us an assemblage of migratory birds present in each level 1 habitat type. Only six habitat types contained assemblages of 10 or more species and only these assemblages were taken forward in the analyses: artificial terrestrial (50 species); forest (33 species); grassland (38 species); savannah (40 species); shrubland (49 species); inland wetland (25 species). Many species have multiple habitat associations, and therefore occur in more than one habitat assemblage.

National population trends and imputation of missing values

National-level estimates of population trends were extracted from the European Red List of Birds (BirdLife International 2015). These data were split into long-term (1980–2012) and short-term (2001–2012) bird population trends. Data were extracted for each species in each European country within the East Atlantic flyway where data were available, and prepared following Sanderson et al. (2016). Countries were considered to be within the flyway if their centroid fell within the flyway boundary (BirdLife International 2010). As not all countries reported on all species present, and missing data were not distributed at random across species or countries, missing data were multiply imputed with chained equations using the ‘mice’ package 2.22 (Buuren and Groothuis-Oudshoorn 2011) in R 3.2.3 (R Development Core Team 2015). This approach specifies a multivariate imputation model, variable by variable, using a set of conditional densities, drawing imputations by iterating over these densities (Buuren and Groothuis-Oudshoorn 2011). This allowed us to impute a number of missing data points in the response variables. Full details are given in Appendix S1 and comparisons of observed and imputed data are shown in Figs. S1 and S2. The result was 10 versions of a complete dataset, each with differing estimates of the values missing from the
original dataset, allowing the uncertainty around the true missing values to be incorporated into subsequent analyses. All subsequent analyses were performed on each of the 10 datasets independently, and the results pooled, following the methods of Buuren and Groothuis-Oudshoorn (2011).

**Population trends across Europe**

Europe-wide population trends for each species were calculated as an average of national trends, with each trend weighted by the national population estimate as a proportion of the total population estimate for all European countries within the flyway (BirdLife International 2015). This ensured that changes in larger national populations had a larger impact on the overall trend than changes in smaller populations.

BirdLife International’s species distribution polygons were then used to map each species’ population trend onto its non-breeding distribution in sub-Saharan Africa. For each 0.5° grid cell, we then calculated an “assemblage trend index” per habitat type as the mean population trend value across all species occurring in that cell in that imputation. The rationale is that if species’ population trends reflect environmental changes in their African wintering grounds, areas where declining species co-occur in winter (i.e. areas with a low index value) are likely to be those where adverse environmental changes are taking place.

**Phenology data**

Phenology data were derived from the NDVI-based VIP-PHEN 0.05-degree Phenology Earth Science Data Record (Didan et al. 2015). This product, developed as part of NASA’s Making Earth System data records for Use in Research Environments (MEaSUREs) project, uses data from multiple sensors spanning the AVHRR and MODIS eras, to provide the longest and most consistent satellite-based measurement of global vegetation phenology currently available (Didan et al. 2015). We extracted data for the years 1981–2012 inclusive. The lack of data prior to 1981 meant there was a slight mismatch between the time periods over which long-term phenology trends and long-term population trends were calculated. However, we consider the influence of missing data from 1979 and 1980 would be very small, given the 31-year continuous period for which data were available.

The VIP-PHEN phenology product summarizes data both annually and seasonally. Each calendar year contains up to three growing seasons, and for each growing season the following parameters are given: start date, end date, length (in days), date of peak NDVI, rate of greening, rate of senescence and maximum NDVI. Additional annual parameters include cumulative NDVI and number of seasons. All data are provided as annual multi-band rasters with a spatial resolution of 0.05°.

As the number of growing seasons per year often fluctuated both temporally and spatially, two reference points of 1 November (day 305) and 1 March (day 60) were used to ensure that data were extracted for the seasons in which migratory species would be present on their wintering grounds. Growing seasons were split into a greening period (from start of growing season to date of peak NDVI) and a senescence period (from date of peak NDVI to end of growing season), and data were extracted for any greening or senescence period that intersected day 60 or day 305.

For greening periods, we extracted start date and rate of greening and calculated length of greening as the number of days between start of season and peak NDVI. For senescence periods, we extracted end date and rate of senescence and calculated length of senescence as number of days between peak NDVI and end of growing season. As our period of interest (November to February) fell across the change in calendar year, to maintain a linear scale we adjusted all start, end and peak dates to be relative to 1 January (day 1), such that any dates falling in the previous year were given negative values (e.g. day 305 became day −60). In addition to these three greening and three senescence variables, we also used cumulative NDVI in the whole of the previous calendar year as an indicator of overall productivity.

**Climate data**

Climate data were obtained from the CRU TS3.10 dataset (Harris et al. 2014), as multi-band rasters mapped at a 0.5° resolution. Six climate variables were extracted for the months of November, December, January and February from November 1981 to February 2012 inclusive, to match the period covered by the phenology data: potential evapotranspiration, precipitation, minimum monthly temperature, mean monthly temperature, maximum monthly temperature and rain days. Mean values per ‘year’ (November to February period) were then calculated for each variable.

**Calculation of trends in phenology and climate**

Long-term (1982–2012) and short-term (2001–2012) trends for all climate and phenology variables were mapped using the ‘green-brown’ package (Forkel et al. 2013) in R version 3.2.3 (R Core Team 2015). We used the annual aggregated time series method and calculated
a single linear trend per pixel across the whole 31- or 12year time series. This produced a set of six climate trend rasters at 0.5° resolution and seven phenology trend rasters at 0.05° resolution, for each time period. Phenology rasters were then resampled to resolution of 0.5° prior to further analysis.

**Statistical analysis**

To allow the relationship between climate and phenology trends and bird population trends to vary spatially across Africa (non-stationarity), we used geographically weighted regression (GWR) models. GWR is a spatial regression technique that constructs a local model with a separate regression equation and associated parameter estimates for every observation in the study area (Charlton and Fotheringham 2009). A weighted window is moved across the entire study area, estimating one set of coefficient values at every chosen ‘fit’ point (Dormann et al. 2007). Nearer observations have a greater weight than distant ones in calibrating the local set of regression parameters, and the size and shape of this relationship is determined by the bandwidth and kernel type (Charlton and Fotheringham 2009). Here, we used a fixed kernel weighting function, where all points within a given distance of the input point were included in the local regression model with equal weight, and the optimal bandwidth distance was determined for each model separately, using a cross-validation method (Fotheringham et al. 2002). GWR models were run in ArcGIS 10.3.1 (ESRI 2015). Although GWR does not explicitly model spatial autocorrelation, it has been shown to have significantly less influence in GWR models, compared to ordinary least squares regressions (Sheehan et al. 2013), thereby reducing the chance of type I errors (Bailey 2016). Residual spatial autocorrelation could be an issue if we were explicitly testing a hypothesis, as non-independence of proximal locations can affect the estimate of standard errors. However, we used GWR here as an exploratory tool rather than to draw conclusions based upon the testing of hypotheses.

Before running GWR models, we checked for multicollinearity across all climate and phenology trends, identifying correlated pairs of variables as those having a Pearson correlation coefficient of 0.7 or higher. GWR has shown to be more sensitive to local collinearity than global models (Bailey 2016). For each pair of correlated variables, we excluded the variable that was least correlated with the assemblage trend index for the same time period, starting with the variable with the lowest index correlation. This resulted in the exclusion of long-term trends in potential evapotranspiration, mean monthly temperature and rain days, and short-term trends in minimum monthly temperature, maximum monthly temperature and rain days. A correlation matrix of environmental trends is given in Table S2.

Three multivariate GWR models were run for each habitat type for each time period: one containing climate trends, one containing greening trends and one containing senescence trends. Trend in cumulative NDVI was included in both the greening and senescence models. All models were run at a resolution of 0.5° and had either long- or short-term assemblage trend index as their dependent variable.

Model performance was assessed using $R^2$, adjusted to compensate for the number of variables in the model. We also considered the bandwidth derived from cross-validation as an indication of the geographic scale over which variables acted, and the Moran’s I statistic of the model residuals, as a measure of residual spatial autocorrelation. Spatial autocorrelation in the residuals could indicate a poorly specified or a poorly fitted model.

One of our aims was to look at spatial variation across the flyway in relationships between assemblage trend indices and environmental conditions. For each input point in the model, GWR outputs point-specific estimates of coefficients, along with their standard deviations, for each of the independent variables in the model. We used these to calculate 95% confidence intervals around each coefficient estimate, and identified where these confidence intervals did not overlap zero. We recognize that there remains the potential for type I errors due to potential underestimation of the 95% CI arising from residual spatial autocorrelation. Consequently, these outputs should be considered as indicative products of an exploratory analysis, rather than as a hypothesis test of where there are significant relationships between population change and environmental conditions.

**Results**

**Assemblage trend indices**

Mean assemblage trend indices showed similar geographic patterns in the long- and short term, although more species were found to be declining in the short term (43) compared to the long term (38) (Table S1). Across most of the sub-Saharan flyway area, assemblage trend indices were below 1, indicating mean species declines (Fig. 1). The assemblages with the greatest long-term declines were in the northern Sahel [grassland, shrubland and artificial (farmland) species], and in southern Africa (savanna, shrubland and especially wetland and grassland species). There were areas where the assemblage trend indices were above 1 (indicating on average populations of species occurring in these areas had increased), across all habitat types and in both the long- and the short term. This was
particularly notable in the humid tropical zone south of the Sahel, for all habitat groupings except grassland and wetland (Fig. 1). There was geographical variation in the number of species associated with each habitat type (Fig. S3), but there were no obvious associations between the number of species and either the magnitude or direction of the assemblage trend indices. Mapping the standard deviation of assemblage trend indices across imputations showed that across both time periods and all habitat types, variation was greatest in the northern Sahel (Fig. S4). In general, variation was greater in the long-term than in the short-term trends, reflecting the higher proportion of missing values in the long-term trend data (40.3%) compared to the short-term trend data (27.5%) (Fig. S4).

Correlates of population change

The $R^2$ values from the GWR models indicated that, at a flyway-wide scale, the variables relating to climate and senescence (i.e. the die-back of vegetation after the growing season) explained the greatest proportion of total variance in both long- and short-term trend indices across all habitat types (Table 1). In the long term, the climate model explained slightly more variation than did the senescence model, whereas in the short term, the opposite was true, apart from for grassland and wetland species (Table 1). However, the Moran’s I statistics showed that there was substantial spatial autocorrelation in the residuals of all models, suggesting that none of the models were able to adequately account for the spatial variation in the assemblage trend indices.

Optimum bandwidths differed between the models, with bandwidth for the climate and senescence models always being smaller than the bandwidth for the greening models. Consequently, in order to make direct comparisons between adjusted $R^2$ values of different models, we also re-ran the models using the mean optimal bandwidths from all models (3.99 for long-term models, 4.55 for short-term models). In the long-term, the climate models still explained a greater proportion of variance across all habitat types than either the senescence or greening models (Table 2).

To assess the relative importance of the variables in each of our climate, greening and senescence models, we re-ran the models excluding one variable at a time and compared the adjusted $R^2$ values of the models including and excluding that variable. To allow $R^2$ values to be compared directly, we used a fixed bandwidth equal to the mean optimal bandwidth of the model with all variables included.

For the long-term climate models, in all habitat types, removal of rain days resulted in the greatest reduction in adjusted $R^2$ (1.5–3.3% of total variance; Table 3). In the short-term models, the greatest reductions in adjusted $R^2$ were seen with removal of precipitation in forest and shrubland habitats (1.8–2.5% of total variance) and with removal of mean temperature for all other habitats (1.1–2.2% of total variance; Table 4).

For the long-term greening models, removal of cumulative NDVI resulted in the greatest decrease in adjusted $R^2$ across all habitat types (0.9–1.9% of total variance; Table 3). Removal of start date and rate of green-up from the short-term model resulted in an increase in adjusted $R^2$ in the majority of habitat types, while removal of cumulative NDVI again resulted in the greatest decrease in adjusted $R^2$ (0.5–3.2% of total variance; Table 4).

In the long-term senescence models, removal of end date resulted in an increase in adjusted $R^2$ across three habitat types, while removal of cumulative NDVI resulted in the greatest decrease in adjusted $R^2$ (0.5–2.1% of total variance) for all habitat types except forest (Table 3). In the short-term models, removal of end date increased

Figure 1. Long-term (1981–2012) and short-term (2001–2012) assemblage trend indices for each of the six habitat associations. All values are averaged across 10 imputations to account for missing data. Values less than 1 indicate wintering species assemblages with mean population declines per species. Values greater than 1 indicate wintering species assemblages with mean population increases per species.
Table 1. Summary statistics for multivariate geographically weighted regression models linking long-term and short-term assemblage trend indices for Afro-Palearctic migrants with trends in climatic and phenological variables.

| Model       | Habitat   | Long term |          |          |          |          | Short term |          |          |          |
|-------------|-----------|-----------|----------|----------|----------|----------|------------|----------|----------|----------|
|             | Bandwidth (dd) | Adjusted $R^2$ | Moran’s I | Bandwidth (dd) | Adjusted $R^2$ | Moran’s I |
| Climate     | Artificial  | 2.55      | 0.820    | 0.0476   | 3.14      | 0.720    | 0.0464    |
|             | Forest     | 2.55      | 0.809    | 0.0635   | 3.14      | 0.727    | 0.0546    |
|             | Grassland  | 2.55      | 0.825    | 0.0712   | 3.14      | 0.837    | 0.0456    |
|             | Savanna    | 2.55      | 0.825    | 0.0521   | 3.14      | 0.838    | 0.0382    |
|             | Shrubland  | 2.55      | 0.871    | 0.0464   | 3.14      | 0.807    | 0.0404    |
|             | Wetland    | 2.55      | 0.841    | 0.0709   | 3.14      | 0.802    | 0.0769    |
| Greening    | Artificial  | 7.07      | 0.491    | 0.0550   | 7.81      | 0.433    | 0.0386    |
|             | Forest     | 7.07      | 0.553    | 0.0627   | 7.81      | 0.563    | 0.0286    |
|             | Grassland  | 7.07      | 0.588    | 0.0772   | 7.81      | 0.653    | 0.1156    |
|             | Savanna    | 7.07      | 0.549    | 0.0734   | 7.81      | 0.646    | 0.0662    |
|             | Shrubland  | 7.07      | 0.634    | 0.0665   | 7.81      | 0.670    | 0.0603    |
|             | Wetland    | 7.07      | 0.568    | 0.0804   | 7.81      | 0.653    | 0.1588    |
| Senescence  | Artificial  | 2.25      | 0.814    | 0.0740   | 2.69      | 0.775    | 0.1432    |
|             | Forest     | 2.92      | 0.701    | 0.1500   | 2.69      | 0.745    | 0.1808    |
|             | Grassland  | 2.24      | 0.804    | 0.0645   | 2.69      | 0.835    | 0.1096    |
|             | Savanna    | 2.24      | 0.841    | 0.0883   | 2.69      | 0.862    | 0.0943    |
|             | Shrubland  | 2.24      | 0.862    | 0.0794   | 2.69      | 0.835    | 0.0860    |
|             | Wetland    | 2.24      | 0.797    | 0.1007   | 2.69      | 0.785    | 0.1684    |

All values represent means across 10 imputations. dd = decimal degrees.

Table 2. Summary statistics for fixed bandwidth multivariate geographically weighted regression models linking long-term and short-term assemblage trend indices for Afro-Palearctic migrants with trends in climatic and phenological variables.

| Model       | Habitat   | Long term |          |          |          |          | Short term |          |          |          |
|-------------|-----------|-----------|----------|----------|----------|----------|------------|----------|----------|----------|
|             | Bandwidth (dd) | Adjusted $R^2$ |          |          |          |          | Bandwidth (dd) | Adjusted $R^2$ |          |          |
| Climate     | Artificial  | 3.99      | 0.747    |          |          | 4.55      | 0.652    |
|             | Forest     | 3.99      | 0.735    |          |          | 4.55      | 0.649    |
|             | Grassland  | 3.99      | 0.748    |          |          | 4.55      | 0.786    |
|             | Savanna    | 3.99      | 0.768    |          |          | 4.55      | 0.799    |
|             | Shrubland  | 3.99      | 0.823    |          |          | 4.55      | 0.759    |
|             | Wetland    | 3.99      | 0.773    |          |          | 4.55      | 0.738    |
| Greening    | Artificial  | 3.99      | 0.657    |          |          | 4.55      | 0.531    |
|             | Forest     | 3.99      | 0.714    |          |          | 4.55      | 0.660    |
|             | Grassland  | 3.99      | 0.723    |          |          | 4.55      | 0.778    |
|             | Savanna    | 3.99      | 0.677    |          |          | 4.55      | 0.721    |
|             | Shrubland  | 3.99      | 0.743    |          |          | 4.55      | 0.736    |
|             | Wetland    | 3.99      | 0.717    |          |          | 4.55      | 0.798    |
| Senescence  | Artificial  | 3.99      | 0.712    |          |          | 4.55      | 0.643    |
|             | Forest     | 3.99      | 0.637    |          |          | 4.55      | 0.581    |
|             | Grassland  | 3.99      | 0.698    |          |          | 4.55      | 0.729    |
|             | Savanna    | 3.99      | 0.763    |          |          | 4.55      | 0.793    |
|             | Shrubland  | 3.99      | 0.790    |          |          | 4.55      | 0.760    |
|             | Wetland    | 3.99      | 0.686    |          |          | 4.55      | 0.640    |

All values represent means across 10 imputations. dd = decimal degrees.
adjusted $R^2$ except for shrubland species, while removal of cumulative NDVI caused the greatest decrease (0.1–0.7% of total variance) in all habitat types except artificial (Table 4).

Thus, overall, the non-spatial contributions of individual climate and phenology variables to the GWR models are relatively small, in comparison to the total amounts of variance explained by the models, suggesting that the majority of the variance was explained by spatial elements. Of the non-spatial elements, rain days (i.e. the frequency of rain) appeared to have some influence on the long-term trends, while in the short-term trends, precipitation and mean temperature appear to be of some importance. However, cumulative NDVI was perhaps the most important variable overall in both the long- and short-term trends.

### Spatial patterns of relationships between change and environmental variables

The apparently large contribution of the spatial component to the GWR models indicates that there is considerable spatial variation in the relationships. The outputs of GWR models allow the distribution and direction of relationships between dependent and independent variables to be mapped. This in turn allows us to examine geographical variation in correlations between assemblage trend indices and climate and phenology across the flyway. Overall, similar patterns of association were seen in the long- and short-term trends (Figs. 2 and 3; Figs. S5–S10). Associations with climate variables were widespread and highly spatially variable across all habitat types in both the long- and short-term trends (Figs. 2 and 3;
Figs. S5–S10). In general, climate variables appeared to have most influence in southern Africa and the humid tropical zone south of the Sahel (Figs. 2 and 3).

Across habitat types, greening variables appeared to have most influence in southern Africa, especially in the short-term trend. There was a consistent pattern for longer periods of green-up in southern Africa to be associated with higher assemblage trend indices across all habitat types (Figs. S6 and S7). Relationships with other greening variables were more variable, both spatially and between habitat types, although in the short term, there was a tendency for higher assemblage trend indices to be associated with a later, slower, longer green-up, often with lower cumulative NDVI (Fig. S6).

Figure 2. Relationships between long-term assemblage trend indices of Afro-Palearctic migrant species from 1980 to 2012 and trend in climate, greening and senescence variables, as determined from multivariate geographically weighted regression models. Maps show proportion of model variables significant at each location, based on mean results from 10 models representing 10 imputations of missing data.

Figure 3. Relationships between long-term assemblage trend indices of Afro-Palearctic migrant species from 2001 to 2012 and trend in climate, greening and senescence variables, as determined from multivariate geographically weighted regression models. Maps show proportion of model variables significant at each location, based on mean results from 10 models representing 10 imputations of missing data.
Associations with senescence variables tended to be more localized than associations with greening variables, which had broader distributions (Figs. S7–S10). This is no doubt a reflection of the smaller optimal bandwidths of the senescence models (Table 1). In both the long- and short-term trends, senescence variables were notably significant across the Sahel and sub-Saharan region (Figs. 2 and 3). For forest, shrubland and artificial (farmland) species, more positive assemblage trend indices in the long-term trend were associated with a shorter but slower senescence, ending later, and with higher overall cumulative NDVI (Fig. S9).

With the exception of length of green-up in relation to the long-term trends, none of the climate or phenology variables were found to have a consistent relationship with assemblage trend indices for any species groups across the whole flyway. Instead, there was considerable spatial variation in the direction of significant relationships, with most variables having both positive and negative relationships with assemblage trend indices in different geographic areas (Figs. S5–S10).

**Discussion**

We mapped, for the first time, the mean population trends of migratory species onto their non-breeding distributions in sub-Saharan Africa and used geographically weighted regression models that account for non-stationarity to examine correlations between assemblage population trend indices and changes in climate and vegetation phenology over the same period. Our results suggest that the relationships between population trends of migratory species and climate and phenology are spatially variable and far more complex than previous studies (e.g. Ockendon et al. 2014) have suggested.

Mapping the population trends of migratory species onto their non-breeding distributions using our assemblage trend indices suggested that species wintering in southern Africa (and to some extent the northern Sahel) had the greatest mean declines per species, both in the long- and short-term trends. As we used a single population trend per species, these patterns are due to differences in species composition of migrants between areas. In contrast, species occurring in the humid tropics of West Africa on average showed population increases in both the long- and short-term trends. These findings differ from those of Atkinson et al. (2014), who found that populations of species wintering in the Sahel are generally stable or increasing, but those which use the Sahel only as a staging area are in decline. This suggests that more attention should perhaps be given to migratory species using the drier habitats of southern Africa, as well as to grassland species, which were the habitat group for which declines were greatest.

There was considerable and intricate spatial variation in relationships between assemblage trend indices and environmental characteristics. However, one clear pattern was the relationship between assemblage trend indices and senescence in the Sahel and sub-Saharan areas of the flyway. The relationships with both long- and short-term trends and the end of senescence, rate of senescence, length of senescence and cumulative NDVI appeared broadly consistent across multiple groups of species, especially those associated with structural habitats (forest, savanna and shrubland). These relationships could indicate that species’ populations increased more (or decreased less) where senescence happened later, and was shorter but slower when it did happen (potentially resulting in higher cumulative NDVI). This suggests that later and less pronounced seasonal changes in this region could be beneficial to migratory species.

In southern Africa, green-up appeared to play an important role. In general, species increased more (or decreased less) when green-up started later and was longer and slower, with lower cumulative NDVI. Again, this may suggest that overall, less dramatic changes in seasons are more important than absolute values of NDVI. It could be that there is an optimal pattern in the growing seasons, with sustained green-up being important for species arriving in southern Africa, and sustained presence of green vegetation (i.e. later, slower senescence) being important for species as they pass back through the Sahel region on their return journey north. Together, these patterns might indicate again that different drivers have caused changes in populations of species with different habitat associations in different parts of Africa.

Seasonal patterns of climate and vegetation growth in Africa are strongly influenced by the oscillation of the inter-tropical convergence zone (ITCZ) throughout the year (Schneider et al. 2014). Many migrants time their arrival in Africa to coincide with the rainy season and resource-track throughout the non-breeding season, following the ITCZ south as it brings drought-breaking rains and associated flushes of vegetation and insects to new areas (Trierweiler et al. 2013; Thorup et al. 2017). If senescence happens before birds arrive on wintering areas, the number of insect preys could be lower. This might in turn force birds to move to new areas. If these are further south, birds might depart for spring migration in poorer condition, or spend longer at stopover sites, delaying return to breeding grounds (Bell 2007; Tøttrup et al. 2012). Recent tracking studies have revealed that several species wintering further south pass through western Africa on their spring migration route (Åkesson et al.
2012; Cresswell and Edwards 2013; Willemoes et al. 2014; Evens et al. 2017), meaning conditions there towards the end of the non-breeding season could be key in determining resource availability at stopover sites. This is consistent with our finding that earlier senescence in the Sahel region was associated with lower assemblage trend indices in the long term for shrubland, forest and artificial (farm-land) species.

Although cumulative NDVI explained the greatest proportion of variance in the majority of greening and senescence models, other characteristics relating to the timing, rate and duration of greening and senescence also contributed to explaining residual variance. These relationships suggest that measuring cumulative NDVI alone is simplistic. Additionally, we found that relationships between assemblage trend indices and cumulative NDVI are not uniform across the flyway, and are not always positive (i.e. in different parts of the flyway, assemblage trends can increase or decrease with increasing NDVI).

The absence of a single continent-wide association between climate or phenology and assemblage trends in our analysis suggests that detailed assessments are required to understand how population trends relate to conditions in Africa. Considering the continent or flyway as a whole, or using broad spatial units as has been done in many previous studies (e.g. Balbontin et al. 2009; Robson and Barriocanal 2011; Ockendon et al. 2012, 2014; Morrison et al. 2013; Finch et al. 2014), may mask processes occurring at finer scales.

Relating phenology changes derived from remotely sensed data to bird population changes across an area as large and diverse as the East Atlantic flyway in sub-Saharan Africa presents a number of challenges. Considering the remotely sensed data first, in many places, the number of growing seasons varied or fluctuated between years, as well as between neighbouring pixels, making comparisons difficult. To standardize comparisons, we introduced reference dates relating to the core period in which migrants were expected to be present, and split the growing season to consider greening and senescence separately. However, this approach meant that in areas where greening had finished by 1 November and did not start again until after 1 March, which included the Sahel, the influence of greening could not be assessed directly, but only through its influence on the timing, length and rate of senescence, which did fall within the focal study period.

However, the greatest limitation in our analysis undoubtedly arose from the paucity of data on the distribution and population trends of migrants in Africa. Satellite remote sensing means we are now better able to assess land cover condition than populations and distributions of birds. Even within Europe, data on population trends of migrants were missing for a relatively high number of species-country combinations, especially in the long-term. Although we accounted for missing trend data using an imputation method, which reduces bias in estimated trends where data are not missing completely at random, this introduced extra uncertainty into our analysis, and therefore greater errors than had a complete dataset been available. Our knowledge of area-specific population trends of migrants during the non-breeding season is even more limited, although recent work demonstrates the feasibility of establishing monitoring schemes capable of this in Africa (Wotton et al. 2017). In addition, although we used the best available maps of species’ non-breeding distributions, these vary greatly in accuracy between species, as the wintering distributions of many migrants are still poorly known.

This lack of data made it necessary to make a number of assumptions about the non-breeding distributions of migrant species. Firstly, that species’ ranges had not changed across years (1980–2012), despite changes in vegetation and climate, or within years, for example, as itinerant species track resources (Thorup et al. 2017). We also assumed that each species consisted of a single population with complete mixing on wintering grounds, even if breeding populations were known to be discrete, an assumption that seems relatively realistic given recent evidence that low connectivity may be common in long-distance migrants (Finch et al. 2015, 2017; Hewson et al. 2016). The extent to which these assumptions are realistic is difficult to assess, but we believe they are likely to have added variation rather than systematic bias to our data. Despite these caveats, this study represents an important first step in bringing together long-term population trend data of migrants in Europe with remotely sensed data on changes in vegetation and seasonality across species’ wintering ranges in Africa.

Better data on the non-wintering populations and distributions of migrants, including improved knowledge of their migratory connectivity (Cresswell 2014) and within-season movements, are needed to fully determine the extent to which they may be impacted by changes in conditions in Africa. With advances in satellite remote sensing and the tools available to process data at high spatial and temporal resolutions, the limitation is no longer in the availability of environmental data, but in our knowledge of the non-breeding ecology of migrants. This gap in knowledge can only be addressed through fieldwork in non-breeding areas, and the use of new and emerging tracking technologies to identify migratory pathways and help target this fieldwork (Vickery et al. 2014).

A recent rise in the use of tracking technologies has already begun to greatly improve our understanding of
species’ migratory routes and use of stopover and wintering sites (Åkesson et al. 2012; Cresswell and Edwards 2013; Willemoes et al. 2014; Evens et al. 2017; Finch et al. 2017). If we are to take advantage of these opportunities and make best possible use of these data as they emerge, cooperation and collaboration will be required. The seabird tracking community are leading the way, with collation of data in a centralized tracking database (seabirdtracking.org) enabling identification of global priorities (Lascelles et al. 2015). An equivalent database for migratory landbirds would be a big step forward. Combining this information with satellite-derived vegetation and phenology data, such as that synthesized in this study, could be a powerful tool in understanding the influence of phenology throughout the entire lifecycle of migrants. It could also reveal the extent to which species are flexible in their choice of wintering grounds, and whether distributions change between years and/or within seasons, in relation to environmental conditions. Until then, we suggest that it is no longer assumed that there is a straightforward relationship between migrant populations and NDVI across species’ ranges, and that studies should, at the very least, consider the multiple attributes of phenology and the potential for spatial variation in relationships.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Imputation of missing values

Table S1. Species included in analyses, their presence (1) or absence (0) in each of the six habitat assemblages, and their mean long-term (1981–2012) and short-term (2001–2012) population trend indices (averaged over 10 imputations to account for missing data).

Figure S1. Comparison of long-term (1981–2012) species trends calculated using non-missing (observed) values only and missing (imputed) values only, for each of six habitat groupings.

Figure S2. Comparison of short-term (2001–2012) species trends calculated using non-missing (observed) values only and missing (imputed) values only, for each of six habitat groupings.

Figure S3. Total count of Afro-Palearctic species, by habitat group, wintering across the sub-Saharan part of the East Atlantic Flyway.

Figure S4. Standard deviation in each of the six habitat
assemblage trend indices across 10 imputations to account for missing data. Long-term trends are for the period 1981–2012. Short-term trends are for the period 2001–2012.

**Figure S5.** Relationships between long-term assemblage-trend indices of Afro-Palearctic migrant species from 1981 to 2012 and trend in precipitation, minimum monthly temperature and frequency of rain, as determined from multivariate geographically weighted regression models. Maps show mean results from 10 models representing 10 imputations of missing data.

**Figure S6.** Relationships between long-term assemblage-trend indices of Afro-Palearctic migrant species from 2001 to 2012 and trend in potential evapotranspiration, precipitation and mean monthly temperature, as determined from multivariate geographically weighted regression models.

**Figure S7.** Relationships between long-term assemblage-trend indices of Afro-Palearctic migrant species from 1981 to 2012 and trend in start date, rate and length of green-up and cumulative NDVI, as determined from multivariate geographically weighted regression models.

**Figure S8.** Relationships between long-term assemblage-trend indices of Afro-Palearctic migrant species from 2001 to 2012 and trend in start date, rate and length of green-up and cumulative NDVI, as determined from multivariate geographically weighted regression models. Maps show mean results from 10 models representing 10 imputations of missing data.

**Figure S9.** Relationships between long-term assemblage-trend indices of Afro-Palearctic migrant species from 1981 to 2012 and trend in end date, rate and length of senescence and cumulative NDVI, as determined from multivariate geographically weighted regression models. Maps show mean results from 10 models representing 10 imputations of missing data.

**Figure S10.** Relationships between long-term assemblage-trend indices of Afro-Palearctic migrant species from 2001 to 2012 and trend in end date, rate and length of senescence and cumulative NDVI, as determined from multivariate geographically weighted regression models.

**Appendix S2.** Correlation of environmental trends.

**Table S2.** Pearson correlation coefficients for correlations between climate and phenology trends. Values above the diagonal break relate to long-term (1981–2012) trends.