Examining the temporal synchroneity between migratory bird arrival and spring phenology in the UK

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Abstract

Anthropogenic climate change is having cascading effects throughout ecosystems on macro to micro scales, as organisms attempt to shift their timing to match local climates. Migratory birds are particularly at risk as their survival is dependent on synchronising arrival timing with a small window of optimal spring phenology events. Several migratory species have been found to be arriving earlier at breeding sites across Europe; however, little evidence has been reported of UK breeding species, with no prior multispecies research investigating the extent of phenological mismatch in the UK. With the use of 356,900 unique phenological observations spanning multiple taxa from 2000-2021, this study explored if 4 migratory bird species synchronised arrival with UK spring phenology over the past two decades. Of the 10 indicators included in the spring index, 60% exhibited advancing phenology and the spring index demonstrated significant correlation with spring temperature. Of the avian species, willow warblers exhibited the most adaptive migration in response to the advance in spring. Conversely, swifts demonstrated increasingly delayed arrival in relation to the spring index and therefore experienced the most phenological mismatch over this study period. These findings highlight the ranging adaptive ability of avian species to climate change. Additional research into the migratory mechanisms driving interspecific variance in adaptive ability to climate change would be beneficial to implement effective conservation strategies to those failing to synchronise arrival with spring phenology.

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First and foremost, I would like to thank Dr Andrew Hacket-Pain who made this dissertation project possible. His guidance, encouragement and invaluable knowledge enabled me to develop this project idea into a reality.

I would like to thank my mum and dad, who raised me to have a fascination for the natural world. I owe this project to them and our annual tradition of completing the garden bird survey together. I would also like to thank my friends at home and university for their support and encouragement during this process.

Lastly, I would like to extend my gratitude to the Nature's Calendar database for providing the data that made this research possible.

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List of Abbreviations

NC – Natures Calendar (Woodland Trust, 2024)

DOY – day of year

SI – Spring Index

ROC – rate of change

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1. Introduction

Phenology is defined as the timing of recurring biological events in an organism's life cycle (Lieth, 1974). The biological process is highly responsive to the cumulative effects of temperature change over time and has been used as a climate proxy throughout human history (Schwartz, 2013). Recent phenological research has highlighted an observed global scale correlation between advancing spring phenology and warming temperatures (Walther et al., 2002; Menzel et al., 2006; Schwartz, Ahas and Aasa, 2006). Migratory birds are also responding to changing climatic conditions through shifts in range and arrival timing (Mayor et al., 2017). However, complexities are arising as some migratory species are increasingly mistiming their arrival with optimal spring phenology, therefore threatening their reproductive success and individual fitness (Saino et al., 2010; Visser and Gienapp, 2019).

Climate induced phenological shifts will have broad ecological consequences, disrupting species interactions, population dynamics and ecosystem functionality (Parmesan, Root and Willig, 2000; Parmesan and Yohe, 2003; Thackeray et al., 2010). Adaptive ability to environmental change differs between species, resulting in varied phenological timing in both direction and magnitude of change (Parmesan, 2007; Both et al., 2009; Roslin et al., 2021). Consequently, certain species are at increasing risk of population decline if climate change persists into the near future, with hundreds of bird species projected to be driven to extinction (Jetz, Wilcove and Dobson, 2007; Saino et al., 2010).

1.1. Phenology

Phenology is an intricate biological mechanism, controlling the timing of key life cycle events such as flowering, migration and breeding. The process supports ecosystem structure and interaction by synchronising the activities of different functional groups in a community, from decomposers to predators (Morellato et al., 2016; Piao et al., 2019). The timing of phenological events is driven by two key mechanisms: ultimate mechanisms and proximate mechanisms (Forrest and Miller-Rushing, 2010; Park and Post, 2022). Ultimate mechanisms are shaped by natural selection and life-history evolution of organisms to adapt their life cycles and maximise reproductive success and survival (Visser et al., 2010). This evolutionary adaption is often to enable organisms to better detect and respond to environmental change (Ramirez-Parada et al., 2024). For instance, Balasubramanian et al. (2006) found evidence for genetic adaption in the plant *Arabidopsis thaliana* (thale cress) via allelic variation in the photoreceptor (the gene locus which is sensitive to light) enabling the plant to be more responsive to photoperiod (day length) and flower earlier. Conversely, proximate mechanisms encompass the external environmental cues, such as temperature, photoperiod and rainfall, which trigger the expression of phenological traits (Forrest and Miller-Rushing, 2010; Park and Post, 2022), often described as phenotypic plasticity in literature. Fox et al. (2019) defined plasticity as “the ability of an individual genotype to produce different phenotypes in response to the environment”. This allows organisms to rapidly adjust behaviour or physical traits in response to abiotic factors, without requiring evolutionary change (Gienapp, Leimu and Merilä, 2007; Primack et al., 2009; Mayor et al., 2017). Phenotypic plasticity is becoming increasingly relevant with climate change, with Ramirez-Parada et al. (2024) demonstrating plasticity as the primary driver of flowering phenology amongst 1605 flowering species across the US.

The timing of spring phenology is crucial to enhance species' reproductive success and survival by synchronizing key life cycle events with favourable environmental and ecological conditions (Visser and Gienapp, 2019). For example, plant-pollinator interactions depend upon the spatial and temporal alignment of flowering and pollinator activity, with entomophilous angiosperms synchronising flowering with peak pollinator activity to maximise reproductive success (Hegland et al., 2009). Similarly, avian species frequently time breeding to coincide with periods of resource abundance and optimal habitat conditions to maximise fitness and reproductive success (Harrington, Woiwod and Sparks, 1999; Møller, 2013; Mayor et al., 2017). However, the timing of spring phenology is a delicate balance of trade-offs. Earlier onset of phenology will extend the growing or breeding season but risks individual fitness from increased exposure to harsh climatic conditions or limited resource availability (Constant et al., 2024). For example, plants which advance spring phenology risk damage to leaf tissue from spring frosts (Augspurger, 2013) but benefit from prolonged carbon intake and reduced interspecific competition (Keenan et al., 2014). Conversely, delaying phenology can improve immediate survival chances (Constant et al., 2024), but risks reduced competitive success for territory or mates, and mismatched reproduction with periods of greatest food abundance, resulting in reduced reproductive success (Visser et al., 1998; Saino et al., 2010).

1.2. Migratory Phenology

Bird migration is a key biannual phenological event where avian species undergo seasonal movements between wintering and breeding grounds, driven by resource abundance and environmental conditions (Somveille, Rodrigues and Manica, 2015). The evolutionary driver of migration is for avian species to maximise reproductive success and juvenile survival by nesting in areas with abundant resource availability (Visser, Holleman and Gienapp, 2005). However, the mechanisms controlling migration are considerably more complex than those governing lower trophic level phenological events. Weak teleconnection between wintering and breeding grounds making it challenging for birds to accurately anticipate breeding ground conditions (Both and Visser, 2001). Differences in migration strategies and adaptive ability are evident among species and individuals, influenced by the following factors: overwintering location, migration route and speed, population size, and demographic traits like age and sex (Tryjanowski and Sparks, 2001; Sorte et al., 2013). For example, Hagan, Lloyd-Evans and Atwood (1991) found that tropical-wintering species primarily migrate in response to photoperiod-triggered endogenous cues, with minimal influence from climatic conditions. Additionally, males typically exhibit r-selected traits, expending energy to optimise the reproductive benefits of an earlier arrival, whereas females exhibit K-selected traits and arrive later at the breeding site, prioritising energy conservation (Morbey and Ydenberg, 2001; Schmaljohann, Eikenaar and Sapir, 2022). Climate change poses a significant threat to many migratory bird species by disrupting arrival synchrony with breeding ground conditions, heightened by their inflexible phenotypic plasticity, with widespread population declines reported across Europe (Berthold et al., 1998; Both et al., 2006).

1.3. Shifting phenological trends and mismatch

In recent decades, an extensive number of reports have documented an earlier onset of spring phenological events in response to climate change (Piao et al., 2019), with a 1.1°C increase in global temperatures relative to pre-industrial levels (IPCC, 2023). These shifts are driven by species' ability to rapidly adjust to changing environmental conditions through phenotypically plastic behavioural responses (Charmantier and Gienapp, 2013; Ramirez-Parada et al., 2024) and occasionally rapid evolution, as seen in avian species (Berthold et al., 1992). Memmot et al (2007) reported a direct correlation between advancing spring phenology and temperature over the past century, with flowering and insect emergence advancing by 4 days per 1°C increase in temperature temperate zones. Meta-analyses spanning 16-132 years of time-series data for a multitude of taxa estimate the global average advancement of spring phenology in terrestrial regions to be between 2.3 to 5.1 days decade^{-1} (Parmesan and Yohe, 2003; Root et al., 2003; Cohen, Lajeunesse and Rohr, 2018). The ranging estimates of global phenological advance could be due to a multitude of factors, including the effects of climatic differences among time periods, latitudinal differences in data, and taxa included in the metanalyses (Badeck et al., 2004). Parmesan (2007) also remarked about the importance of consistent analysis methodologies between metanalyses to produce globally reliable results.

The Northern Hemisphere has undergone particularly rapid warming over the past century (IPCC, 2023). The greatest warming has typically been exhibited in winter and spring months, and consequently phenological advancements has been most pronounced for spring events (Menzel et al., 2006; Schwartz, Ahas and Aasa, 2006; Schwartz, 2013; Post, Steinman and Mann, 2018). Meta analyses by Menzel et al. (2006), across Europe, and Parmesan (2007), across the Northern Hemisphere, reported an average spring advancement of 2.5 and 2.8 days decade^{-1} respectively. Spring advancement trends have been observed to occur on a latitudinal gradient for phenological events in plants including budburst, leaf unfolding and flowering (Jeganathan, Dash and Atkinson, 2014; Roslin et al., 2021), and migration and nesting in birds (Sparks and Braslavska, 2001). This has been evidenced in the Arctic where spring advancement rates are as high as 30 days per decade due to regional warming occurring almost four times faster than the global average (Høye et al., 2007; Rantanen et al., 2022). However, some analyses have detected a deceleration or even reversal of advancement trends since the start of this century, hypothesised as a response to a global warming hiatus (Piao et al., 2019). The global warming hiatus refers to the stabilisation of global temperature trends which contributed to the widespread slowing or reversal of phenological advancements during spring and autumn (Wang et al., 2019). For example, satellite derived advancement rates decreased from 5.2 days (1982-1999) to 0.2 days (2000-2008) average across the northern Hemisphere (Jeong et al., 2011).

Higher trophic levels have exhibited a less pronounced advancement of spring phenology across the Northern Hemisphere than lower trophic levels, such as plants and insects (Thackeray et al., 2010; Thackeray et al., 2016). For example, Newson et al. (2016) reported an average arrival advancement of 2.2 days decade^{-1} for 11 UK migratory birds, slightly lagging behind the spring advancement trends of 2.5-2.8 days decade^{-1} (Menzel et al., 2006; Parmesan 2007). In migratory birds, the rate at which arrival time shifts is determined by a multitude of biotic factors and abiotic factors, including genetic variance and environmental conditions at both the overwintering site and along the migration route (Gienapp, Leimu and Merilä, 2007; Saino et al., 2010). Tryjanowski and Sparks (2001) also identified avian population size as a significant determinate of arrival time due to the increased probability of an individual detecting shifting external conditions which trigger endogenous cues. However, this relationship is statistically bias since larger population sizes also have a greater probability of being sited earlier at the breeding ground. Despite the statistical bias, this relationship is of growing importance with continued declines in bird populations in recent decades. Substantial declines have been observed from 1995-2022 in swift populations, -66%, and house martins at -44% (BTO, 2014; BTO 2015a). If species mistime their arrival relative to local resource availability, particularly the seasonal abundance of insect prey, they risk ecological mismatch (fig.1). Mayor et al., (2017) undertook the first continental scale asynchrony study, contrasting 48 avian arrival trends with trends of green-up (spring onset) across the US. Their results demonstrated arrival trends increasingly lagging behind green-up trends, with phenological interval (mean absolute effect size) increasing by 5.8 days decade^{-1}. This decoupling between trophic levels can lead to negative fitness outcomes for avian species, including reduced reproductive success and juvenile survival, and ultimately drive population decline (Visser, Holleman and Gienapp, 2005; Visser and Gienapp, 2019).

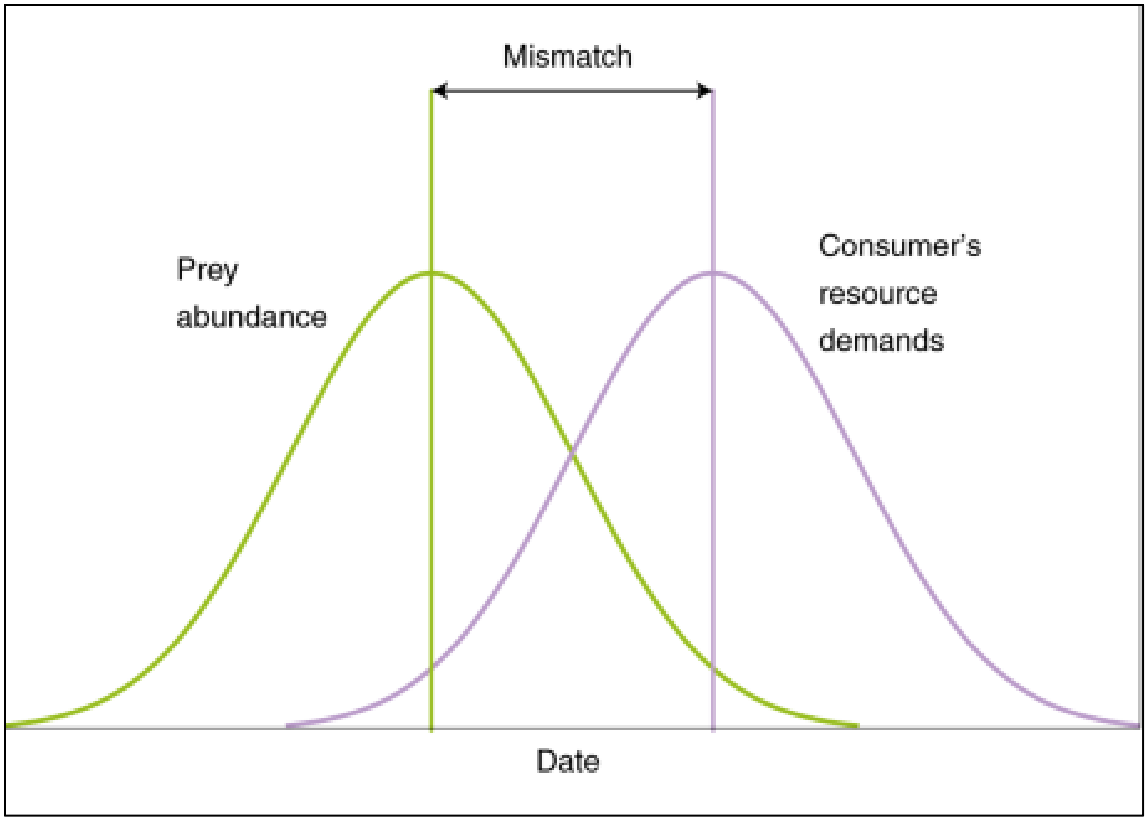

Figure 1. *Graphical depiction of phenological mismatch occurring when consumer mistimes arrival with peak resources abundance. Taken from Visser and Gienapp (2019).*

1.4. Research aims

Following on from numerous multicontinental metanalyses on phenological trends and advancing spring dates conducted at the start of the century (Parmesan and Yohe, 2003; Root et al., 2003; Menzel et al., 2006), this study aims to uncover the recent trends of phenological events specifically within the UK. A similar methodology will be followed to Mayor et al (2017) with the creation of a divergence index to identify if four migratory bird species are effectively timing arrival with the onset of spring. This research is of increasing importance to detect if certain avian species are better adapting to the changing climate so that effective conservation efforts can be implemented to mitigate declining population trends.

This study will examine the temporal synchroneity between spring onset and the arrival of four migratory bird species to the UK from 2000 to 2021, with the use of one of the UK's longest phenology databases – ‘Nature’s Calendar’. This study will first address if spring onset has advanced over the study period by analysing 8 species trends across four phenological events: budburst, first leaf, flowering and insect emergence). These results will be compared with temperature trends over the study period. Arrival trend analyses will then be conducted for the following four migratory bird species: *Delichon urbicum* (hereafter, house martin), *Hirundo rustica* (hereafter, swallow), *Apus apus* (hereafter, swift) and *Phylloscopus trochilus* (hereafter, willow warbler), to determine if arrival trends are shifting at a similar rate to spring onset over the study period. Spring indicators will also be used as a proxy for avian food availability to test for mismatch, similar to the methodology of Mayor et al. (2017), due to the strong correlation between insect emergence and green up. From here, interspecific variance will be assessed to determine if certain species are adapting better to changing environmental conditions.

2. Methodology

2.1. Data collection

Phenological data for 12 unique species across three taxonomic classes were sourced from the Nature's Calendar (Woodland Trust) citizen science database, with observations for the following phenophases: budburst, first leaf, first flowering and first sighting. Phenological data was selected based upon its annual observation size and coverage of the UK. This aimed to reduce the impact of sampling variability as a consequence of the unstandardised methodologies inherent of citizen science databases, as recommended by Primack et al. (2023). Large and well distributed data enhances statistical robustness, increasing confidence that the apparent trends reflect phenological shifts rather than changes in sampling.

This study analyses 21 years of phenological data for each species (2000 – 2021), meeting the minimum threshold of 20 years recommended to detect reliable phenological trends (Sparks and Menzel, 2002). However, the relatively short timeframe within this study could still limit the detection of trends. To mitigate this limitation, Angiosperm and Insecta phenological results will be contextualised with temperature data as a covariate, and all findings will be compared to those of previous relevant studies with longer datasets. To enhance the reliability of the dataset, extensive data handling was conducted, removing 9.88% of the initial 396,028 unique observations. Exclusions included all records prior to 2000 to standardise the time frame across all species, years with insufficient observation (<50 datapoints), and any entries flagged as "rejected" by NC. This resulted in a final dataset of 356,900 observations, with the variance in annual observation for each taxonomic group shown in appendix 1.

2.1.1. Spring indicators

Phenological data from both Angiosperm and Insecta taxonomic classes were analysed over the study period to identify trends in the timing of spring, using the phenological data as spring indicators to create the SI. The following species from the Angiosperm class were assessed: oak (pendunculate), silver birch, blackthorn, bluebell and oxeye daisy, and from the Insecta class: holly blue, peacock and red admiral. These species spring phenology were used as a proxy for avian food availability, following a similar methodology to Mayor et al (2017). Phenological records of budburst (DOY on which the first buds emerge), first leaf (DOY on which the first leaves emerges), first flowering (DOY on which the first flowers emerge), or first sighting (DOY on which the first individual is documented each spring) across the UK were sourced from the NC citizen database. To ensure the reliability of the SI, additional data was excluded from the analysis. All observations of red-tailed bumbles were removed due to insufficient data (<5 observations between 2000 and 2005), and all records prior to 1999 were excluded from the holly blue dataset due to insufficient data (<50 observations). This allowed for robust trend analysis and ensured that all spring indicators aligned to the same time frame (2000-2021).

2.1.2. Migratory birds

Four avian species were analysed to evaluate the interannual and long-term trends in migratory bird phenology within the UK: house martin, swallow, swift and willow warbler. Records of each species' first sighting across the UK were sourced from the NC citizen database. To ensure meaningful interspecific comparison, all avian species included in this study overwinter in Sub-Saharan Africa (fig.2). By using the overwintering region as a control in this study, the pre-migratory variables were standardised as species would respond to similar external migratory cues, including photoperiod and seasonal climatic change. This approach highlights species-specific phenological shifts and mitigates the confounding influence of differing regional environmental cues, in line with Walther et al.'s (2002) recommendations. Furthermore, all avian species selected are insectivorous, meaning that their reproductive success is reliant on the availability of insects. This relationship is crucial for assessing phenological mismatch between the timing of avian arrival and spring onset in the UK.

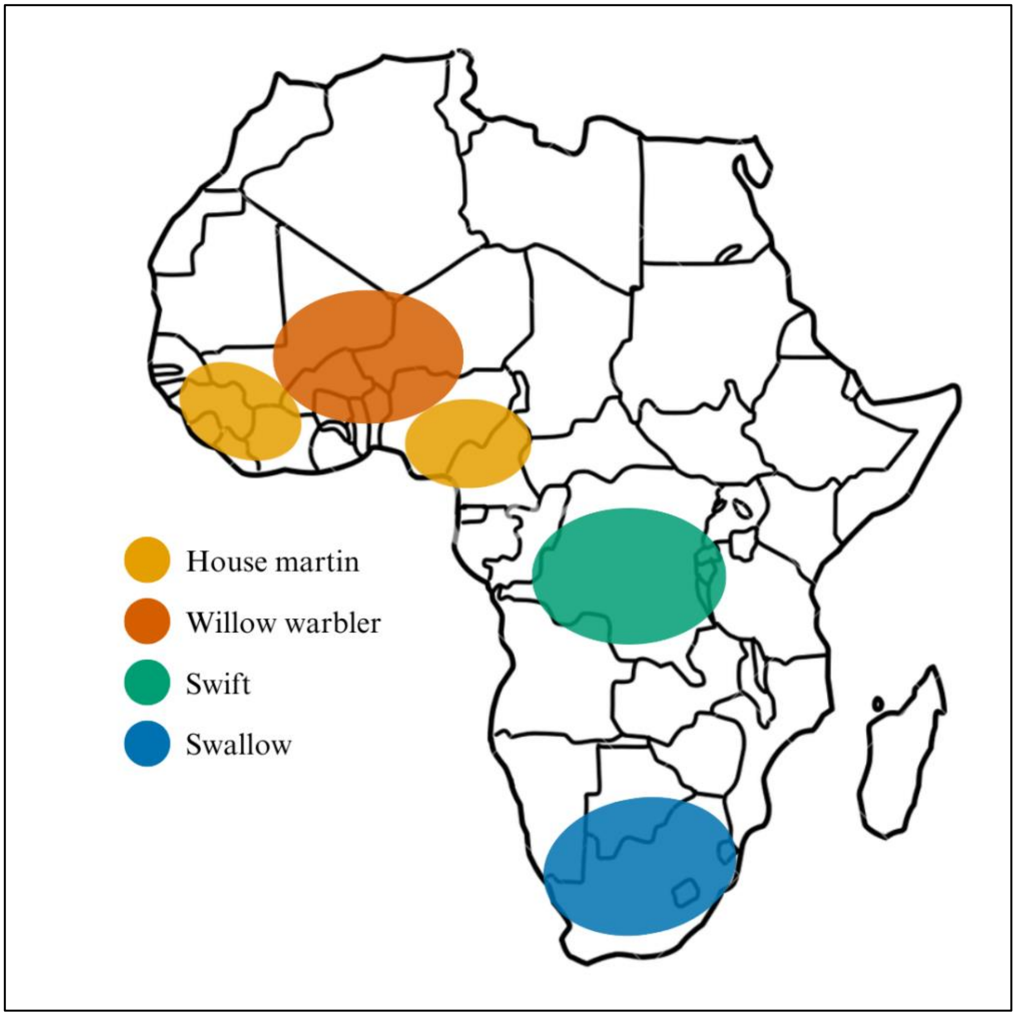

***Figure 2**. Approximate geographical locations of four avian species' overwintering sites across Sub-Saharan Africa created using Canva (2013). The geographical locations are as followed: house martins and willow warblers in Western Africa (Hobson et al., 2012; Lerche-Jørgensen et al., 2017), swallows in South Africa (Pancerasa et al., 2018), and swifts in Congo (BTO, 2012)*

2.1.3. Climate data

To evaluate the relationship between climate variability and phenological trends of spring indicators in the UK, climate data (mean air temperature) at a monthly temporal resolution from 1920 to 2021 was sourced from the Met Office (Met Office, 2024a). Climate data was taken as an average of the UK (fig.3), which could pose as a limitation to this study given the latitudinal variation. This was addressed by restricting the analysis to species with similarly broad geographic distributions, ensuring comparable data. Specifically, winter and spring seasonal temperatures were assessed due to their alignment with the phenophases investigated in this study. Winter temperature was calculated as the mean of monthly temperatures from December to February, and spring temperatures as the mean of monthly temperatures from March to May. Following a similar methodology to Guralnick et al. (2024), the seasonal timeframes provide ecologically relevant climate metrics for this study and avoid the dilution of temperature-phenology relationships with broader temporal windows such as annual temperature.

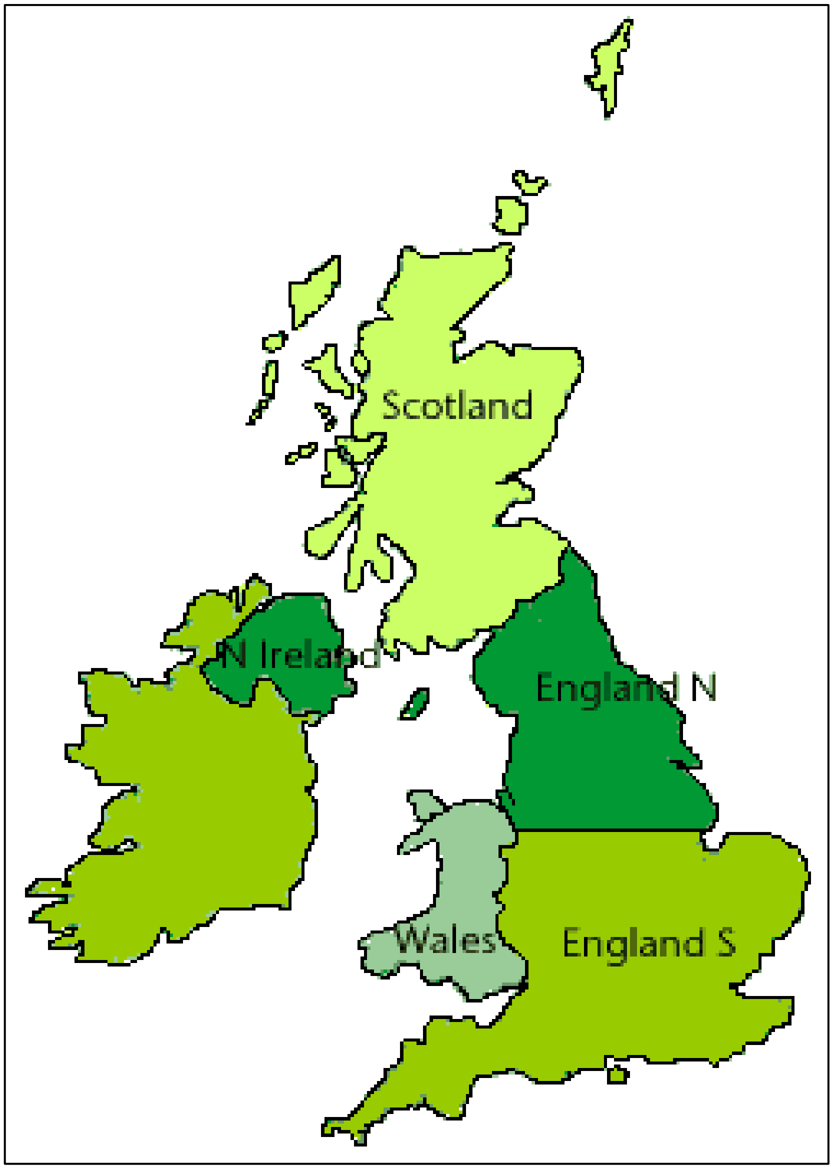

__Figure 3.__ Air temperature data taken as an average from all outlined geographic regions. Sourced from Met Office (2024b)

2.2. Data analysis

Data analysis and presentation were performed using R (Version 2024.12.0+467; R Core Team, 2024) and Microsoft Excel (Version 16.92). The following R packages were utilised for data handling and visualisation: tidyr (v2.1.5; Wickham, 2024b), dplyr (v1.1.4; Wickham et al., 2023), readr (v2.1.5; Wickham, Hester, and Bryan, 2024), and ggplot2 (v2.1.5; Wickham, 2024a). All statistical analyses were conducted at a significance level of $p < 0.05$. Density distribution plots provided an overview of the average arrival times for each avian species in relation to the average onset of spring indicators over the entire study period.

2.2.1. Spring index

The ten indicators of spring were transformed into time-series data by calculating the mean annual onset DOY for each phenophase to evaluate long term trends and relationships with migratory bird arrival, based on the methodology of (Roslin et al., 2021). To enable comparison across species and phenophases, time-series data for all spring indicators were standardised to create a spring index (SI), similar to the index developed by DEFRA (2024) based on phenological data from four UK species (fig.4). Standardisation involved Z-score transformation (using scale() function in R) expressed by the following equation:

$$\mathbf{Z = (\boldsymbol{x} - \boldsymbol{\mu}) / \boldsymbol{\sigma}}$$

Where x is the mean onset DOY for an individual species, μ is the average observation DOY across all indicators, and σ is the standard deviation. For each year, the Z-score of each spring indicator was averaged to produce a single metric representing the timing of interannual spring onset across the UK. Positive SI values indicate a later-than-average spring onset, and negative SI values indicate an earlier onset. The SI remained as a Z-score time-series rather than being converted back to ordinal days to avoid misrepresentation of absolute DOY values due to standardisation effects. The index served as a central metric for assessing the influence of temperature on spring onset and the craetion interannual correlations with migratory bird arrivals, and the potential for phenological mismatch

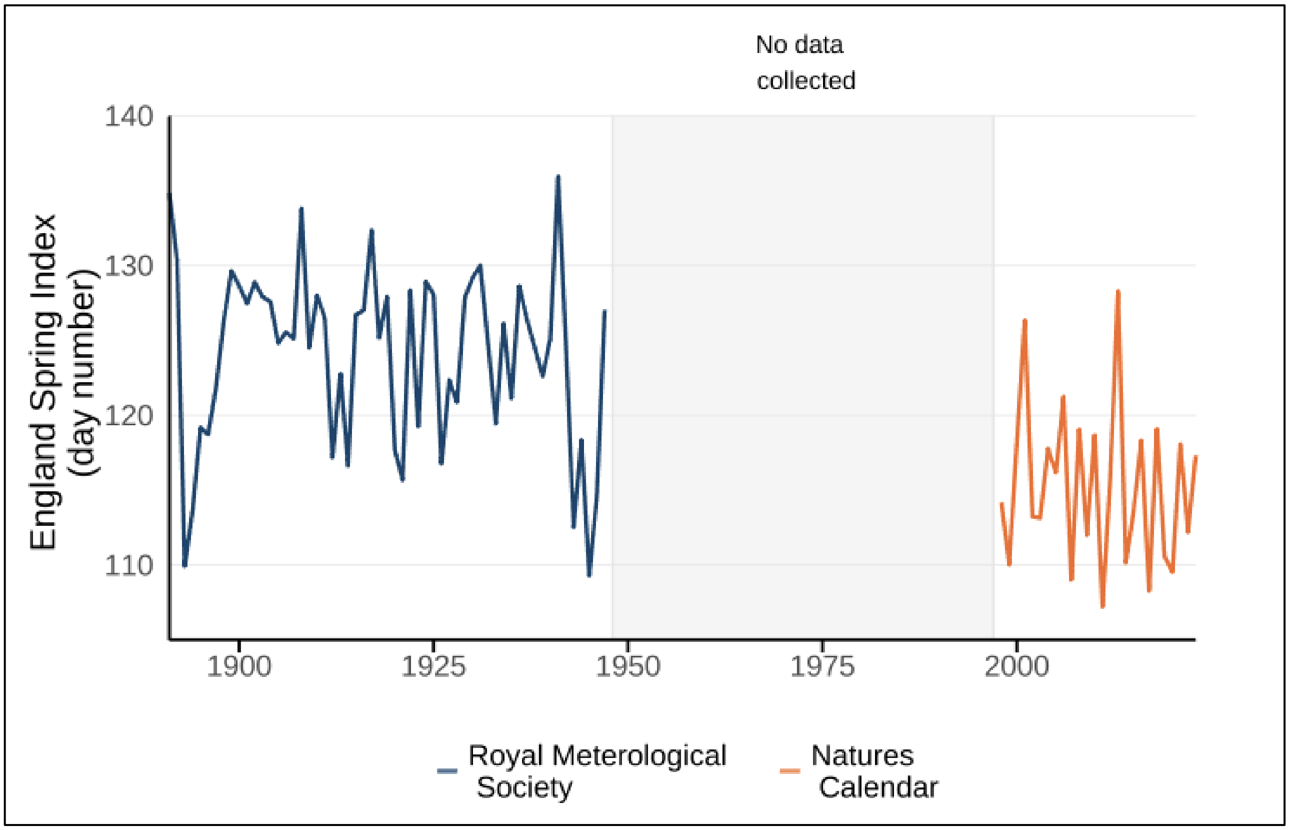

Figure 4. *SI taken from DEFRA (2024) based upon phenological data from four species: first flowering of Crataegus monogyna (hawthorn), first flowering of Aesculus hippocastanum (horse chestnut), first recorded flight of Anthocharis cardamines (orange-tip butterfly), and first sighting of a swallow.*

2.2.2. Effect of temperature

Analyses were conducted to evaluate the effects of winter and spring temperatures on the arrival of spring. Pearson's correlation coefficient was calculated to assess the strength of relationships between the SI and seasonal temperatures for both winter and spring. Additionally, an Analysis of Variance (ANOVA) test was performed to determine which season had a more significant influence on spring onset. This study was limited to evaluating only the effects of temperature on the SI due to the unreliability of using UK temperature data as a proxy for conditions in overwintering habitats which trigger migration (Lehikoinen, Sparks, and Zalakevicius, 2004). To evaluate long term temperature trends, time-series data of the UK's average spring temperature from 1920 to 2000 and 2000 to 2021 were analysed using linear regression analysis. Regression slopes were compared to identify differences between the two periods, with R² and p-values reported to assess statistical significance of the trends.

2.2.3. Rate of change

To assess phenological trends over the study period, the ROC (days per decade) was calculated for each individual indicator. Linear regression models were fitted between the average phenological onset date (DOY) and year to test for temporal shifts in phenological timing, similar to the methodology of Ahas et al. (2002). To provide greater interpretability of results, regression slopes were multiplied by 10 to present the trends as days per decade. 95% confidence intervals were reported to indicate the extent to which the observed trends were statistically distinguishable from zero (Post, Steinman, and Mann, 2018). The inclusion of confidence intervals mitigated the limitations of a shorter study period by providing transparency in results with a clear measure of uncertainty in regression slopes.

2.2.4. Testing for phenological mismatch

Time-series data of the SI was compared with the arrival times of migratory birds across the study period (2000 to 2021) to test for phenological mismatch. A migratory bird index was creating using Z-scores, following the same methodology as the SI. Analyses were conducted across all migratory bird species collectively and then retested at species-level to determine the extent of interspecific variation. Interannual correlation tests were conducted to investigate the association between migratory bird arrivals and spring onset. Pearson's correlation coefficient was used to test the strength of these relationships. Linear regression analysis was conducted to assess long term trends for both the SI and migratory bird arrival times with observation year. Regression slopes were multiplied by 10 to report rates of change as days per decade for each variable. To evaluate the extent of phenological mismatch, a divergence index was calculated for each avian species by subtracting the SI from migratory bird arrival dates, resulting in a divergence time-series. A divergence index of zero indicates that the events are perfectly correlated, and any deviations from zero indicate phenological mismatch. Positive divergence implies earlier bird arrivals relative to spring onset, while negative values indicate delayed arrivals. Temporal trends in divergence were assessed using linear regression to determine if there were significant trends of phenological mismatch.

3. Results

Over the study period from 2000 to 2021, a total of 356,900 individual observations were collected, representing 12 unique species across three taxonomic classes: Angiosperm, Aves and Insecta. From these individual observations, mean annual dates were calculated to establish time series data to track the timing of the following phenological events: budburst, first leaf, first flowering and first sighting. The average arrival of spring occurred on 16th April (ordinal day 106.18 ± 7.12) as indicated by the vernal emergence of flora and fauna from Angiosperm and Insecta phenological data. The earliest spring arrival was recorded on 7th April 2019 (day 96.50), and the latest occurred on 2nd May 2013 (day 121.70). Within the Angiosperm and Insecta classes, species displayed a variability of 57.36 days in spring arrival, with *Prunus spinosa* (hereafter, blackthorn) arriving earliest on 23rd March (day 81.59), and *Leucanthemum vulgare* (hereafter, oxeye daisy) arriving latest on 19th May (day 138.95).

During the study period, the average arrival of migratory birds occurred on 25th April (day 114.86 ± 2.22), which lagged behind the average spring arrival by 8.68 days (appendix 2). Year-to-year variation in avian arrival date was recorded, with the earliest arrival observed in 2011 on day 111.50, and the latest in 2001 on day 119.25. There was considerable interspecific variation among the arrival date of the four avian species studied. On average, willow warblers arrived the earliest on 15th April (day 105.48), and swifts arrived latest on 8th May (day 127.89), approximately 3 weeks (22.41 days) later than the willow warbler (fig.5a-d).

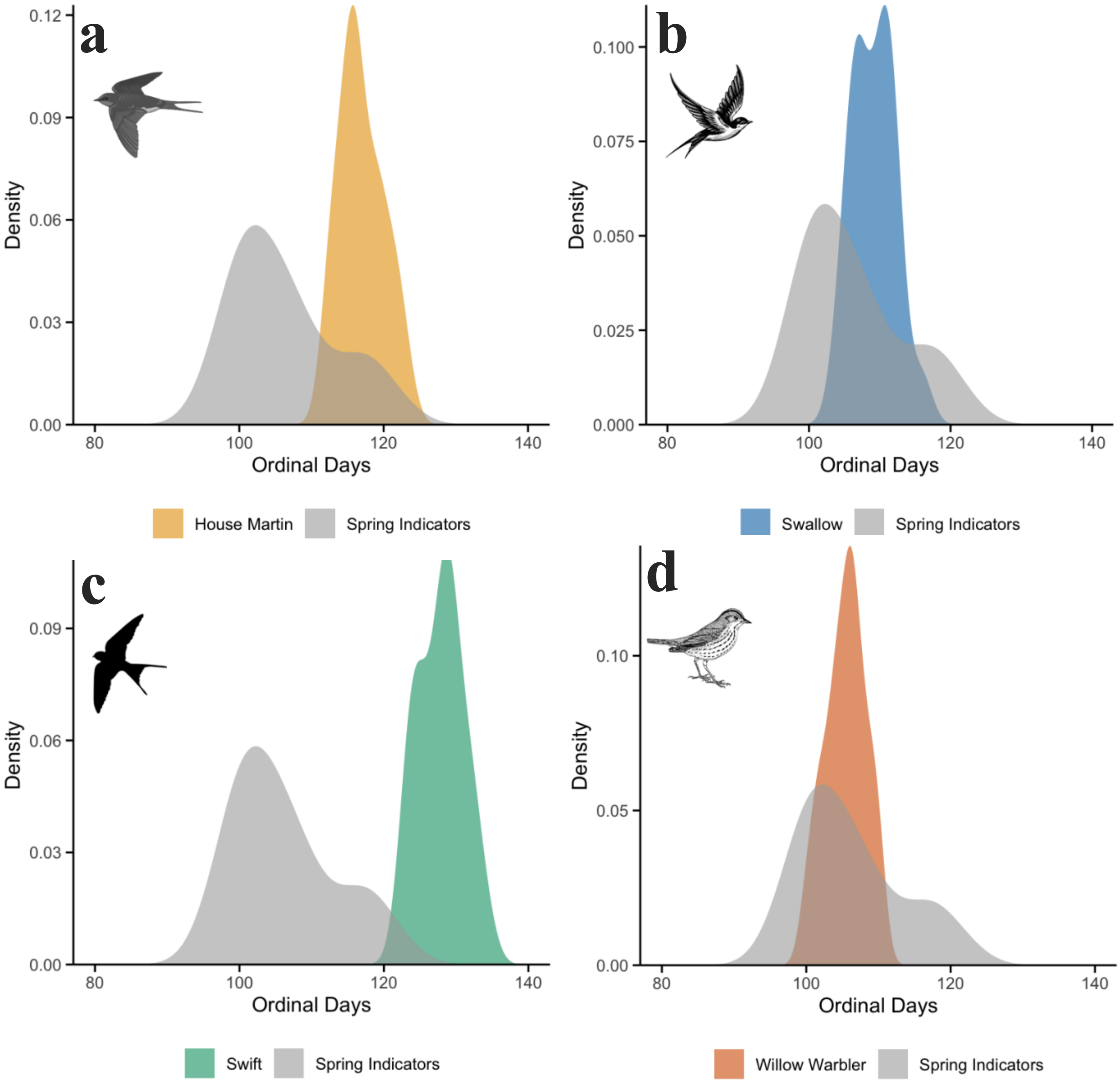

Figure 5. *Comparing the average arrival DOY for four migratory birds with average onset of spring phenology over the study period (2000-2021). a) house martin, b) swallow, c) swift and d) willow warbler.*

3.1. The effect of temperature on spring phenology

In this study, annual spring temperature was a significant driver of spring arrival time as indicated by the SI based on Angiosperm and Insecta time series data (fig.6a). For every 1°C increase in spring temperature, the onset of spring advanced by 0.92 days. Spring temperature accounted for 72% of the variance in the SI ($R^2 = 0.72$), exhibiting a strong and statistically significant negative correlation ($r = -0.85$, $p < 0.001$). Annual winter temperature tested in isolation exhibited a weaker correlation, with an advancement of spring by 0.40 days with every 1°C increase in winter temperature (fig.6b). Winter temperature accounted for 23% of the variance in the SI ($R^2 = 0.23$), with a less pronounced and more variable negative correlation between the variables ($r = -0.48$, $p = 0.024$). Whilst 23% of the variance in spring arrival appears to be accounted for by winter temperature when considered in isolation, an Analysis of Variance (ANOVA) test demonstrates that this association is not significant ($F=2.59$, $p=0.124$). Spring temperature has been identified as the primary driver of spring onset with spring temperature accounting for a significant proportion of the variance in the SI ($F=56.41$, $p<0.001$). These results demonstrate that once spring temperature is accounted for, winter temperature has no residual effect on the arrival of spring.

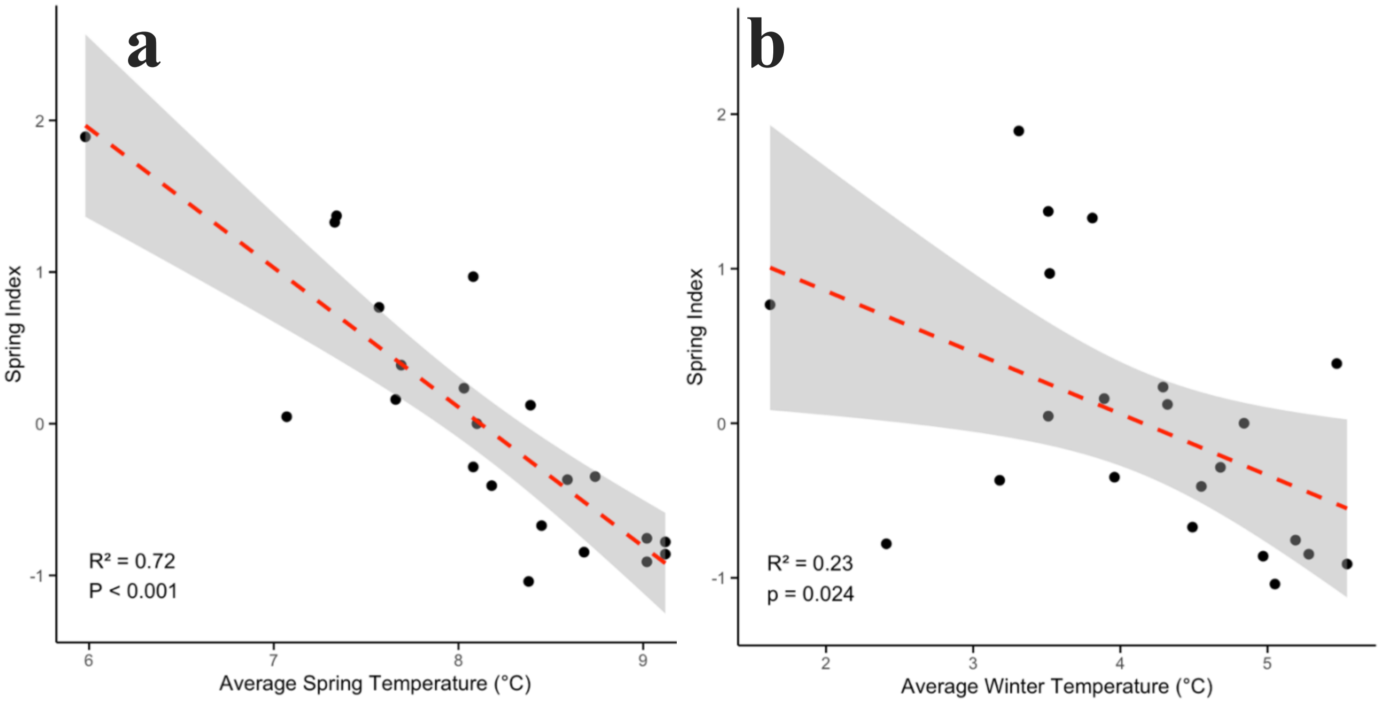

Figure 6. *Correlation between the onset of spring phenology and seasonal mean air temperature in the UK, with points representing annual data, linear trend lines (red dashed) and standard error (grey shaded).* ***a)*** *Effect of spring temperature exhibiting a strong and statistically significant negative correlation ($r = -0.85$, $p < 0.001$).* ***b)*** *Effect of winter temperature exhibiting a weaker and statistically significant negative correlation ($r = -0.85$, $p < 0.001$).*

Time-series analysis of the UK's average spring temperature from 1920-2024 exhibited a statistically significant warming trend, with an annual increase of 0.01ºC year^{-1} ($R^2 = 0.18$, $p < 0.001$; fig.7a). However, when narrowing the assessment to just the study period (2000-2021), no significant spring temperature trend was detected (fig.7b). Over these two decades, spring temperatures exhibited a slight decline by -0.004ºC year^{-1} ($R^2 = 0.001$, $p = 0.87$), suggesting warming trends stabled during this timeframe.

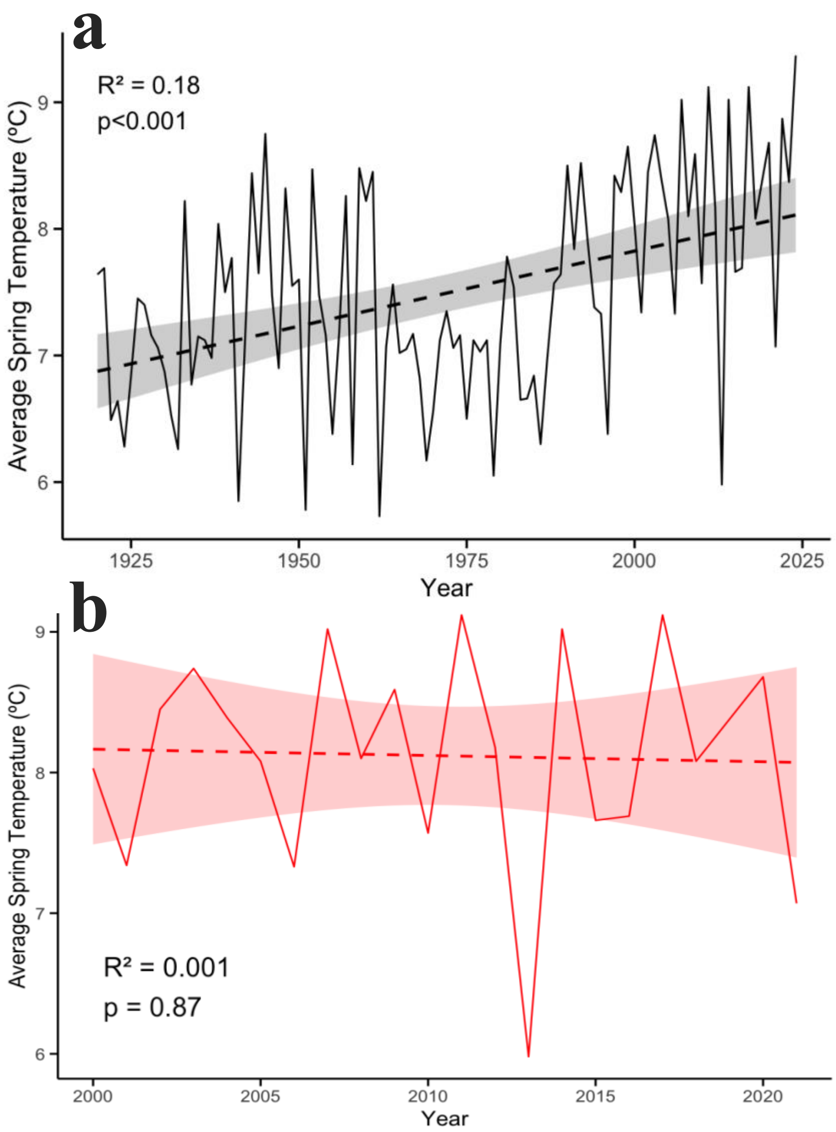

Figure 7. *Correlation between the onset of spring phenology and seasonal mean air temperature in the UK, with points representing annual data, linear trend lines (red dashed) and standard error (grey shaded).* ***a)*** *Effect of spring temperature exhibiting a strong and statistically significant negative correlation (r = -0.85, p <0.001).* ***b)*** *Effect of winter temperature exhibiting a weaker and statistically significant negative correlation (r = -0.85, p <0.001).*

3.2. Phenological trends across taxonomic classes

The timing of phenological events for individual species was assessed over the 21 year study period by calculating the ROC per decade for each species (fig.8). The relatively short study period and large interannual variability of phenological observations limits the statistical power necessary to detect significant phenological trends. Furthermore, UK spring temperatures have shown no trend over the past two decades ($R^2 = 0.001$, $p = 0.87$) which will inevitably shift the size and significance of the phenological trends observed during this study. Nonetheless, invaluable insights into the direction and interspecific variability of phenological shifts across taxa can be attained.

Of the three taxonomic classes tested, swallows were the only species to exhibit a statistically significant trend, advancing by -2.13 days per decade (95% CI: -3.92, - 0.33; $p = 0.03$; table 1), equating to an advancement of more than 4 days over the study period. Despite the limited statistical significance, it is noteworthy that of the ten indicators used to calculate the SI, six demonstrated an advancement of >1 day decade^{-1}. The greatest phenological advancement was exhibited by holly blue of the Insecta class, with its arrival date shifting by -4.02 days decade^{-1} (95% CI: - 10.10, + 2.06; $p = 0.21$). Whilst the majority of spring indicators demonstrated a shift towards an earlier arrival date, there is insufficient evidence to report any as a significant trend within this study period.

Within the Aves class, swallows demonstrated an advancement of 2.13 days decade^{-1}, and house martins and willow warblers showed near to no change. Conversely, swifts demonstrated the greatest delay in arrival time of +1.60 days decade^{-1} (95% CI: - 0.40, +3.61; $p = 0.13$). Despite the limited statistical significance of this trend, it highlights the emerging interspecific variation in shifting phenological trends among the Aves class.

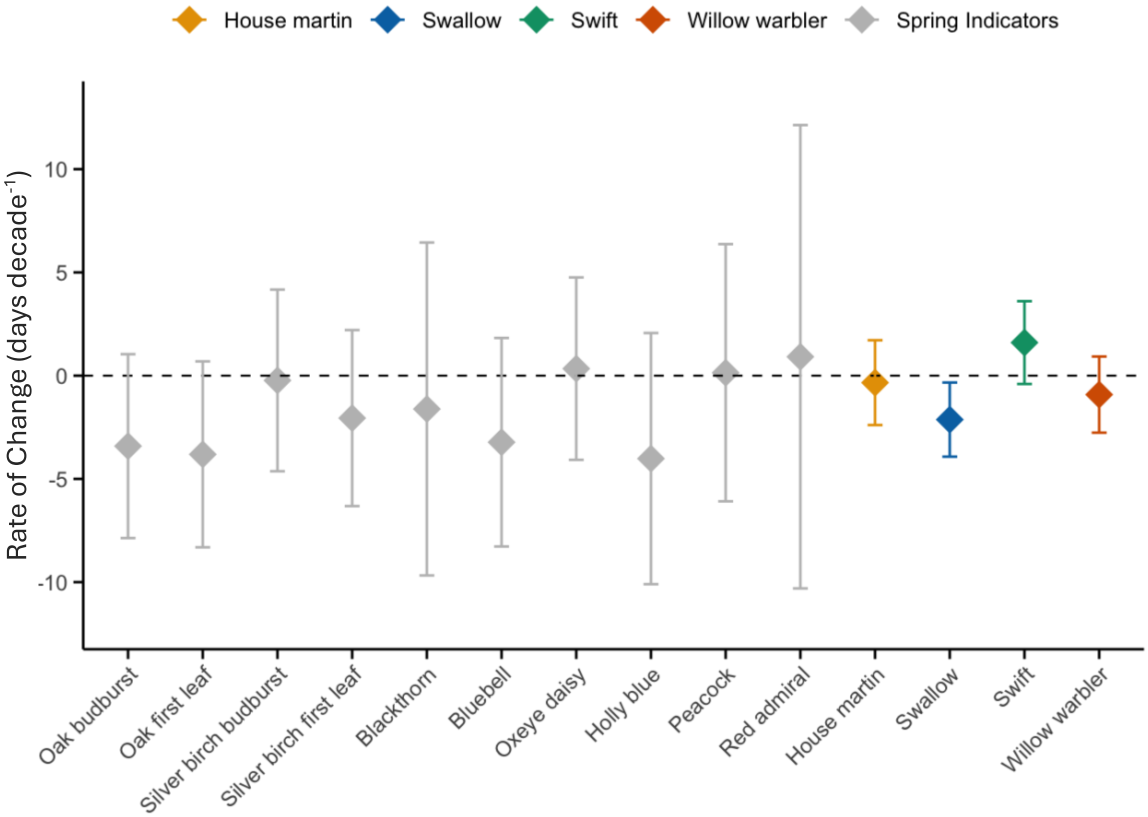

Figure 8. *ROC for twelve individual species over the study period. ROC values calculated from regression slopes of annual phenological data with colours representing species: grey= SI species, yellow= house martin, blue= swallow, green= swift and orange= willow warbler. Positive values indicate delayed phenology, and negative values indicate advanced phenology. Error bars represent the 95% confidence interval of each ROC.*

Table 1. *Statistical output of regression analysis. 'BB' refers to budburst and 'FL' refers to first leaf*

Indicator	ROC (days per decade)	95% CI	p value	Indicator	ROC (days per decade)	95% CI	p value
Oak BB	-3.41	- 7.87, + 1.04	0.15	Holly blue	-4.02	- 10.10, + 2.06	0.21
Oak FL	-3.81	- 8.31, + 0.69	0.11	Peacock	0.14	- 6.09, + 6.37	0.97
Silver birch BB	-0.23	- 4.63, + 4.17	0.92	Red admiral	0.91	- 10.30, + 12.13	0.87
Silver birch FL	-2.06	- 6.32, + 2.21	0.36	House martin	-0.34	- 2.39, + 1.71	0.75
Blackthorn	-1.61	- 9.68, + 6.45	0.7	Swallow	-2.13	- 3.92, - 0.33	0.03
Bluebell	-3.22	- 8.27, + 1.82	0.23	Swift	1.6	- 0.40, + 3.61	0.13
Oxeye daisy	0.34	- 4.08, + 4.76	0.88	Willow warbler	-0.92	- 2.76, + 0.93	0.34

3.3. Testing synchroneity between avian arrival and the SI

The temporal synchroneity between migratory bird arrival and the onset of spring phenology was evaluated using standardised z-scores for phenological events across taxonomic classes. The onset of spring phenology was represented by a SI which standardised the annual vernal emergence of flora and fauna from Angiosperm and Insecta data. This was evaluated against a standardised index of migratory bird arrival to determine the rate and magnitude of phenological shifts over the 21 year study period (fig.9a). The SI demonstrated substantial interannual variability, with the earliest onset of spring events in 2019 (z-score = -1.04), and the latest onset in 2013 (z-score = +1.89). An overall advancement of spring events is observed over the study period as the z-score decreases by -0.22 per decade (95% CI: - 0.78, +0.33). However, the observed trend of a gradual shift towards earlier spring events was not statistically significant (p = 0.43). The arrival of migratory birds exhibited a less pronounced advancement trend, with the z-score declining by -0.16 per decade (95% CI: - 0.78, +0.33), which was also not statistically significant (p = 0.53). Spring arrival accounted for 18% of the interannual variance in migratory bird arrival ($R^2 = 0.18$; fig.9b), exhibiting a moderately weak and statistically significant positive correlation ($r = 0.43$, $p > 0.05$). The moderate correlation suggests that migratory birds are responding to shifts in spring phenology, but not at a fast enough rate to match the shifting onset entirely.

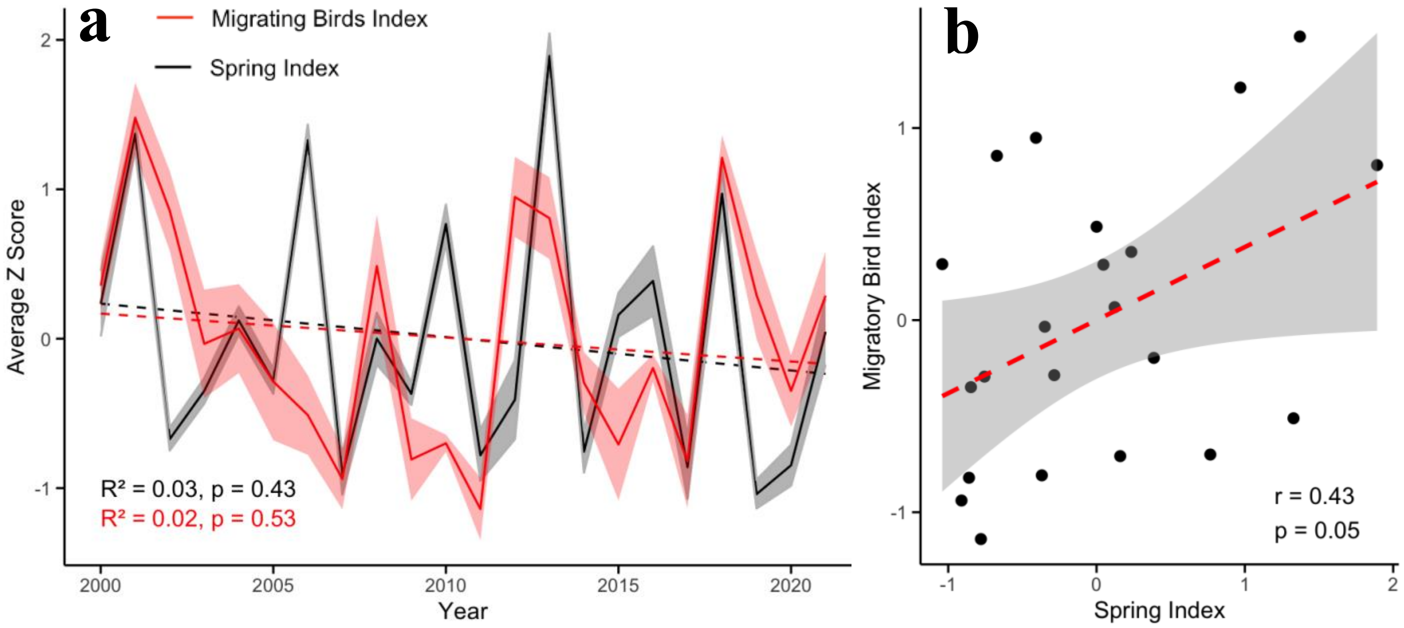

Figure 9. a) *Time-series analysis of the avian arrival index against the SI, with the red line representing birds and the grey representing the SI. Shaded areas represent standard error.* ***b)*** *The moderate correlation between the migratory bird index*

The temporal synchroneity between migratory bird arrival and the onset of spring phenology was further evaluated at the species level (appendix 3a-d). Divergence graphs (avian species z-score – SI) were used to illustrate interannual variations in migratory bird arrival and spring onset, with deviations from zero indicating phenological mismatch. Interspecific variation was evident among the four avian species with differences arising from the long term trends with spring arrival, as well as the strength of correlation with the SI.

a. House martin

House martins exhibit moderate synchrony with the arrival of spring phenology, with occasional substantial deviations from zero indicating phenological mismatch (fig.10a). A divergence of 2.39 was exhibited in 2012, highlighting the species' delayed arrival compared to the onset of spring. No significant temporal trend in divergence was identified ($F_{(1,20)} = 0.084$, $R^2 = 0.004$, $p = 0.77$), with divergence increasing at a rate of 0.01 per year. Spring onset accounted for 6% of the variance in house martin arrival timing ($R^2 = 0.06$, $p = 0.26$), with a weak and not statistically significant positive correlation ($r = 0.25$, 95% CI: -0.19, 0.61, $p = 0.26$; fig.10b).

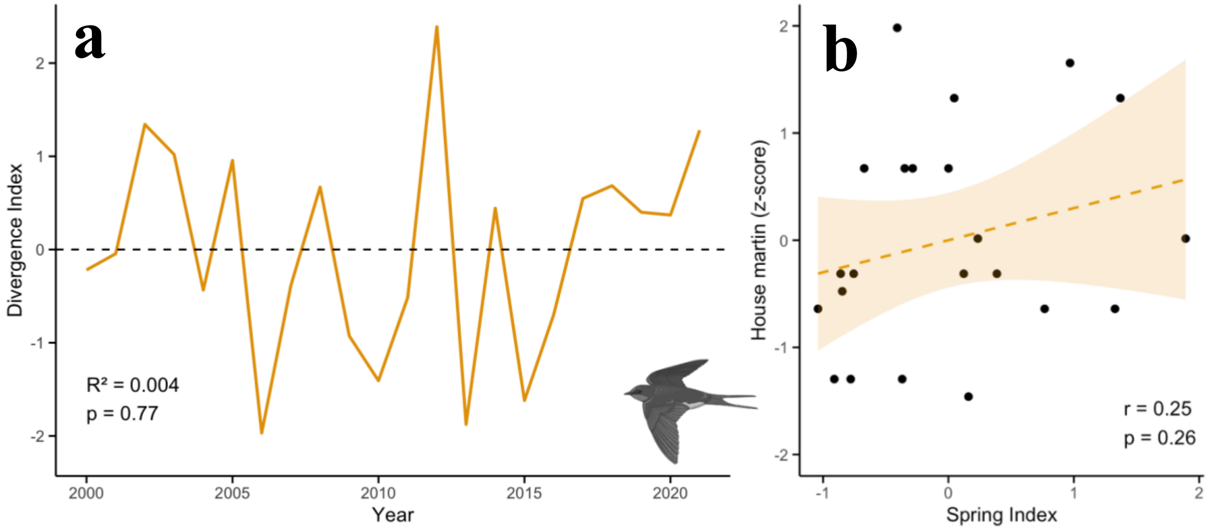

Figure 10. a) *Divergence index calculated as house martin arrival z-score-SI. Positive values indicate late arrival, and negative values indicate early arrival.* ***b)*** *Correlation testing between the house martin arrival and SI.*

b. Swallow

Swallows exhibit moderate synchrony with the arrival of spring phenology, with the divergence index ranging from -2.04 in 2006 to 1.36 in 2012 (fig.11a), indicating occasional phenological mismatch. No statistically significant temporal trend in divergence was identified ($F_{(1,20)} = 1.72$,

$R^2 = 0.079$, $p = 0.20$), however, it is noteworthy that divergence is declining at a rate of -0.05 per year, suggesting a possible shift toward earlier alignment with spring phenology over the study period. Spring onset accounted for 7% of the variance in swallow arrival timing ($R^2 = 0.07$, $p = 0.25$), with a weak and not statistically significant positive correlation ($r = 0.26$, 95% CI: -0.18, 0.61, $p = 0.25$; fig.11b). Swallows demonstrate moderate interannual synchronisation with spring phenology, with some evidence of phenological mismatch.

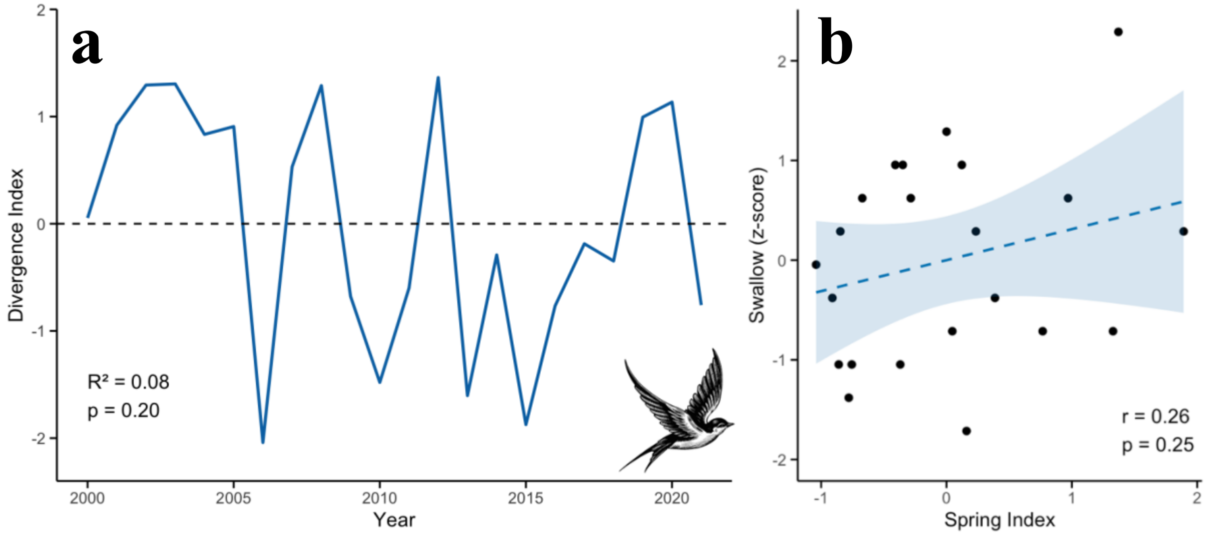

Figure 11. a) *Divergence index calculated as swallow arrival z-score-SI. Positive values indicate late arrival, and negative values indicate early arrival.* ***b)*** *Correlation testing between the swallow arrival and SI.*

c. Swift

Swifts exhibited limited synchrony with the arrival of spring phenology, with sustained periods of substantial deviation from zero indicating phenological mismatch (fig.12a). Divergence ranged between -0.64 and -2.56 from 2003 to 2008, highlighting the species' consistent arrival mismatch within this period. Swifts exhibited delayed arrival over the study period, with divergence increasing by 0.07 per year ($F_{(1,20)} = 3.38$, $R^2 = 0.14$, $p = 0.08$). Whilst the trend was not statistically significant, it highlights the potential for increasing mismatch between swift arrival and spring phenology. Spring onset accounted for 1% of the variance in swift arrival timing ($R^2 = 0.01$, $p = 0.74$), with a very weak and not statistically significant positive correlation ($r = 0.08$, 95% CI: -0.36, 0.48, $p = 0.74$; fig.12b). Swifts demonstrate limited synchronisation with spring phenology on both year-to-year and long-term scales, with evidence of sustained periods of phenological mismatch that could reflect their reliance on different environmental cues or constraints influencing their migratory patterns.

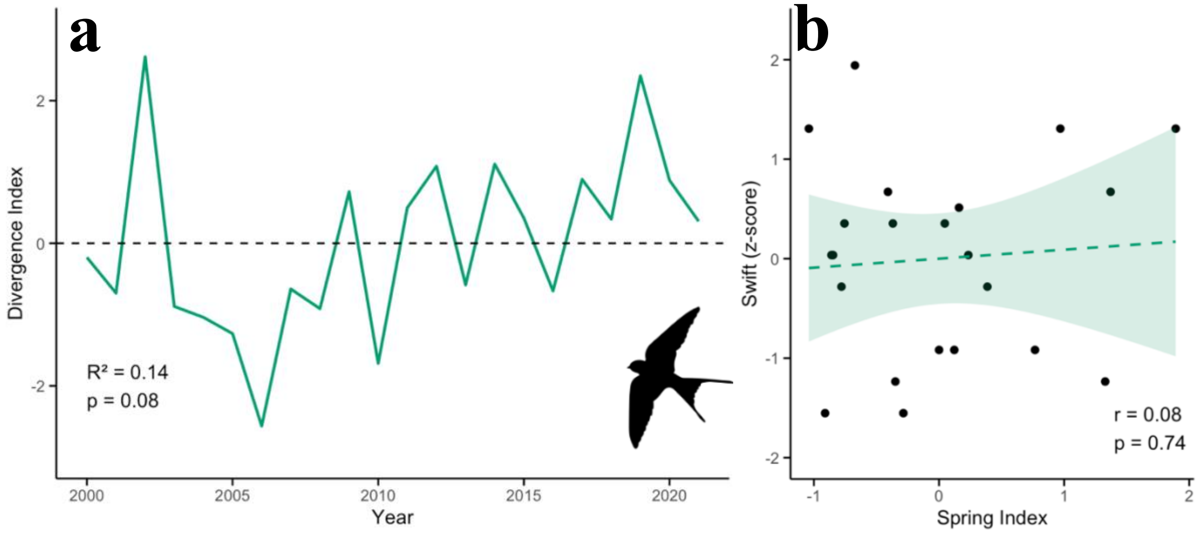

Figure 12. a) *Divergence index calculated as swift arrival z-score-SI. Positive values indicate late arrival, and negative values indicate early arrival.* ***b)*** *Correlation testing between the swift arrival and SI.*

d. Willow warbler

Willow warblers exhibited minimal interannual variance from the onset of spring phenology, with the divergence index ranging from -1.30 in 2010 to 1.58 in 2019 (fig.13a). No significant temporal trend in divergence was identified over the study period ($F_{(1,20)} = 0.167$, $R^2 = 0.008$, $p = 0.69$), with divergence declining by -0.01 per year. Spring onset accounted for 47% of the variance in willow warbler arrival timing ($R^2 = 0.47$, $p < 0.001$), with a strong and statistically significant positive correlation exhibited between arrival time and the SI ($r = 0.68$, 95% CI: 0.37, 0.86, $p < 0.001$; fig.13b). Willow warblers demonstrate effective synchronisation with the arrival of spring phenology and limited phenological mismatch over the study period.

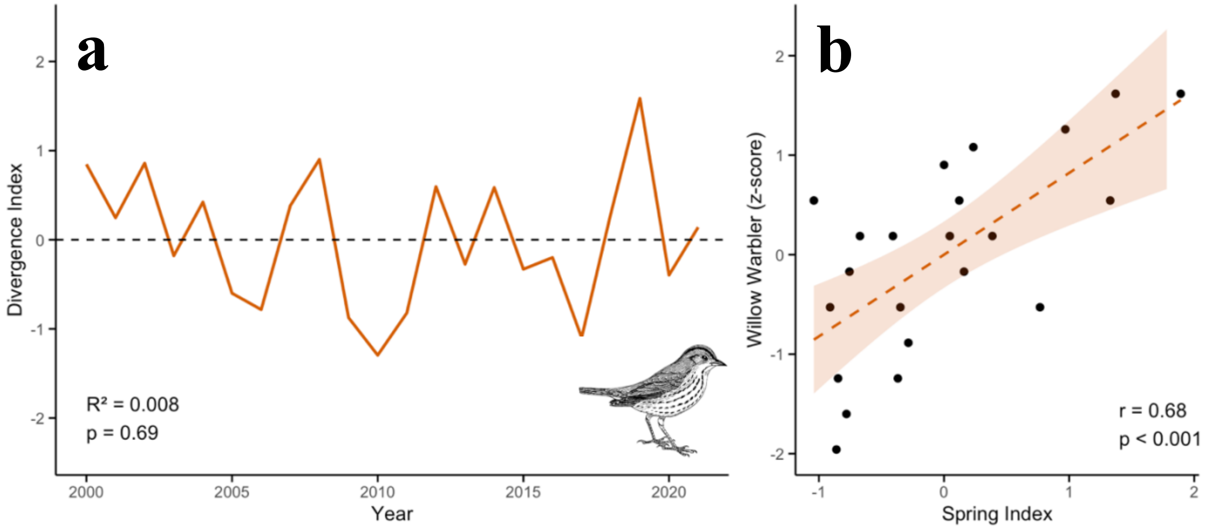

Figure 13. a) *Divergence index calculated as willow warbler arrival z-score-SI. Positive values indicate late arrival, and negative values indicate early arrival.* ***b)*** *Correlation testing between the willow warbler arrival*

4. Discussion

This study aimed to assess the sensitivity of four migratory bird species to shifts in spring phenological timing in the UK and to explore the influence of temperature as a driver of these phenological shifts. The advancement of spring onset, as indicated by the SI, exhibited a strong and statistically significant positive correlation with spring temperature. However, no significant trend in spring temperatures was detected over the study period (2000-2021), contrasting with the pronounced warming trends exhibited in the preceding 80 years (1920-2000). The ROC (days per decade) of the ten indicators used to establish the SI across four phenological events (bud burst, first leaf, first flower and first sighting) exhibited an advancement tendency, with six of the ten indicators exhibiting an advancement of >1 day/decade, and four exhibiting near to no change (0±1 days/decade). However, none of the detected shifts in spring phenology were statistically significant. Large variability was shown across the ROC of the migratory bird species, with swallows exhibiting arrival advancement (>2 days/decade), swifts exhibiting delayed arrival (>1 day/decade), and house martins and willow warblers exhibiting near to no change. Of these detected shifts, only swallows exhibited a statistically significant trend. The association between the SI and migratory bird arrival was tested using linear regression and Pearson’s correlation, with some synchrony being detected, albeit with interannual variability. Substantial variation in sensitivity to spring arrival was detected between avian species, through both divergence of trends and inconsistencies in year-to-year arrival dates relative to spring onset.

4.1. Spring phenology and the effect of temperature

Previous research has established that phenology relies on external environmental conditions, particularly temperature, to determine the timing of life-cycle events (White, Thornton and Running, 1997). Extensive evidence has emerged of an earlier onset of spring phenology in response to climate change (White, Thornton and Running, 1997; Menzel et al., 2006; Schwartz, Ahas and Aasa, 2006). In this study, spring temperature (March-May mean daily temperature) was identified as the dominant driver of spring phenology, aligning with the findings of Chuine and Régnière (2017) identifying spring temperatures critical influence on spring phenology in temperate regions. Over this study period (2000-2021), spring onset advanced by 0.92 days per

1ºC increase in spring temperature. This rate of advancement is weaker than earlier estimates, such as Menzel et al. (2006), who reported a temperature response of 4.6 days per 1ºC across Europe from 1971-2000. These differences likely reflect temporal variations in climate trends, whereby cooler decades will moderate the effect of temperature on phenology.

Winter temperature also plays a role in regulating phenology due to its influence on species' vernalisation processes (Ettinger et al., 2020). If winter temperatures are insufficiently cold, phenological events may be delayed due to disruption to dormancy induction (Tansey, Hadfield and Phillimore, 2017). Cook, Wolkovich and Parmesan (2012) found that 18% of species studied exhibited delayed spring phenology in response to winter warming effects. In this study, winter temperature exhibited a weaker relationship with phenology, showing an advancement of 0.40 days per 1°C increase, but ANOVA testing revealed no statistically significant residual effect of winter temperature on spring onset. Similar results were reported by Geissler, Davidson and Niesenbaum (2023), who found no significant effect of winter temperature on flowering onset from 1884-2015. A metanalyses covering central Europe has reported that chilling effects are unlikely to significantly delay spring phenology unless warming exceeds 4ºC (Ettinger et al., 2020). Therefore, spring phenology will likely continue to advance under current warming trends.

The spring temperature trends observed during this study period (2000-2021) were contrasted with those over the preceding 80 years to provide additional context for phenological trends. From 1920-2000 an overall warming trend was exhibited, with spring temperatures increasing by 0.04ºC per decade. However, the warming trend was reversed over this study period, with spring temperatures declining by -0.05ºC per decade. Historical climate records highlight substantial variability in the 20th century, including a cold period from 1950–70, and two notable warm periods: 1930–45 and 1975–99 (Parmesan and Yohe, 2003). These decadal climate fluctuations are reflected in phenological trends over the century, with the strongest advancement trends arising from studies starting in the late 1970s and ending in the 1990s in response to substantial warming (Sparks and Menzel, 2002; Menzel, 2006; Menzel et al., 2020). Additionally, the start of the 21st century (1998-2012) was characterised by a global warming hiatus, during which global temperature trends stabilised, contributing to the widespread slowing or reversal of phenological advancements during spring and autumn (Wang et al., 2019). The cooling spring temperature trend observed during this study period, along with the well documented warming hiatus, are likely to have suppressed the strength and statistical significance of advancing trends in spring phenology and contributed to the weaker temperature-response relationship observed in this study.

4.2. Shifts in phenology

The analysis of spring phenological events ROC in this study revealed a general tendency towards advancement, with six of the ten spring indicators exhibiting an advancement of >1 day decade^{-1}, and four exhibiting weak change (0±1 day decade^{-1}). However, none of these findings were statistically significant, largely due to the abnormal climate trends over the relatively short study period. Despite this, the observed direction and interspecific variation of phenological shifts are still notable findings and can be contextualised against previous studies.

Within the Angiosperm class, shifting phenology (budburst, first leaf and flowering) ranged from an advancement of 3.81 days per decade (pedunculate oak first leaf) to a weak delay of 0.34 days per decade (oxeye daisy). The pronounced advancement observed in pedunculate oak aligns with previous research highlighting the species' particularly strong adaptive responses to climate change, largely due to lower chilling requirements (Wenden et al., 2019). For instance, Sparks, Carey and Combes (1997) documented an advancement of oak first leaf by 5 days per 1ºC warming. Within this study, approximately 85% of spring indicators within the angiosperm class showed advancing phenology, which is only slightly higher than Menzel et al.'s (2006) global metanalyses reporting phenological advancements in 78% of 542 plant species. The overall mean advance of spring events for the Angiosperm class in this study was 1.55 days per decade. This is lower than previous global metanalyses which reported advancement rates of 2.5 and 3 days decade^{-1} (Menzel et al., 2006; Root et al., 2003). These higher rates of advancement exhibited in earlier phenological studies may be attributed to the stronger warming trends characteristic of their study periods spanning 1971-2000 and 1951-2001 respectively, which will have been mirrored in the intensified phenological trends.

Phenological shifts observed in the Insecta class ranged from an advancement of 4.02 days per decade (holly blue), to a weak delay of 0.91 days per decade (red admiral). Approximately 66%

of butterfly species in this study exhibited delayed arrivals (albeit weakly, at 0±1 day decade^{-1}), resulting in an average advancement of just 0.17 days per decade. Previous phenological analyses on butterfly species documented opposing trends. For instance, Parmesan's (2007) global metanalyses reported an advancement of 3.7 days per decade, and Roy and Sparks' (2001) predicted phenological advancement of 2-10 days per decade ºC^{-1}, based upon 35 British butterfly species from 1976-1998. Interestingly, Roy and Sparks (2001) predicted the red admiral to exhibit one of the strongest phenological advancements (9.2 days per decade ºC^{-1}); however, within this study the species exhibited the greatest delayed in arrival of the Insecta class, at 0.91 days per decade. The uneven ROC across the Angiosperm and Insecta classes in this study could have significant ecological implications, particularly in terms of trophic synchrony. For instance, the pronounced advancement of pedunculate oak (budburst: 3.41, first leaf: 3.81 days decade^{-1}) could desynchronise its interactions with herbivorous insects, as shown in previous phenological studies. Feeny (1970) documented <90% mortality in *Opheroptera brumata* (winter moth) following phenological mismatch between the timing of egg hatching and oak budburst (serving as larval hosts). Beyond the direct consequences on herbivorous insects, the misaligned ROCs could cascade into higher trophic levels, such as reduced prey abundance for bird species (Parmesan, 2007).

Within the Aves class, shifting migratory phenology (arrival date) exhibited considerable interspecific variability over the study period. Of the four migratory birds investigated, swallows exhibited advanced arrival by 2.13 days decade^{-1}, swifts exhibited delayed arrival by 1.6 days decade^{-1}, and house martins and willow warblers exhibited weak advancement of 0.34 and 0.92 days decade^{-1} respectively. Statistical significance ($p<0.05$) was only detected for the arrival trend in swallows, meaning this ROC is particularly noteworthy as it was strong enough to emerge despite the relatively short study period and abnormal climatic trends. The overall mean advancement of arrival dates in this study was 0.27 days decade^{-1}, notably lower than previously reported advancements of 4.3 and 3.7 days decade^{-1} from phenological analyses by Mayor et al. (2017) and Parmesan (2007), respectively. The substantially higher advancement trend of 4.3 days decade^{-1} reported by Mayor et al. (2017) may be attributed to differences in migration distance, as their analyses focuses on species undertaking migration from South to North America, linking back to findings by Saino et al. (2010) that short-distant migrants are exhibiting greater advancement trends than long-distant migrants, such as those in this study. Expectedly, advancement trends for the UK are closer in magnitude to this study. For instance, Newson et al. (2016) reported an average advancement of 2.2 days decade^{-1} across 11 UK migratory bird species, observing that species with the greatest arrival advancements also displayed the most positive abundance trends between 1960-2000. This supports earlier findings by Tryjanowski and Sparks' (2001) of the correlation between arrival timing and increased species abundance. Similar to the Angiosperm and Insecta classes ROC, the substantially lower average advancement of avian species in this study may be partially attributed to the abnormal climatic conditions during the study period. However, community demographics should also be considered when examining trends at a species level.

4.3. Is phenological mismatch occurring?

The extent of phenological mismatch between UK migratory birds and their primary food resource was assessed using the SI as a proxy for insect abundance, an approach supported by prior research demonstrating the comparable temperature thresholds of spring 'green-up' (SI) and insect emergence (Forrest and Thomson, 2011; Visser, Holleman and Gienapp, 2005). Initially, all avian species arrival trends were standardised and compared to the SI. The resulting arrival advancement trend (-0.16 z-score) was less pronounced than the SI (-0.22 z-score), however, both were statistically insignificant, and only 18% of the interannual variance in bird arrival was explained by green-up. These findings indicate that, despite some alignment, the migratory birds in this study are not adjusting their arrival dates quickly enough to match the magnitude of SI advancement. This correspond with Saino et al. (2010) who reported a greater risk of phenological mismatch in long-distance migrants due to their migration being primarily triggered by inflexible endogenous circannual rhythms and photoperiod cues. Similar findings have been detected in North America, with phenological interval (mismatch) increasing by 5.76 days decade^{-1} between 48 breeding passerine species and green-up (Mayor et al., 2017). Phenological mismatch is of particular importance as avian species depend on a short window of optimal habitat conditions and peak resource abundance to maximise fitness and ensure reproductive success (Visser and Gienapp, 2019).

4.4. Variation in sensitivity among species

The interspecific variance in advancement trends reported in this study were expected due to the unique environmental sensitivity and phenotypic plasticity inherent of each species. Furthermore, unique morphological features such as wingspan can affect a species ability to respond to environmental change. Møller, Rubolini and Saino (2017) found a negative correlation between arrival advancement and increasing aspect ratio (species with long, narrow wings) for 80 European migratory bird species, counterintuitively suggesting that these effective flyers are prone to constraints on phenotypic plasticity. This links to the effects of migration routes and stopovers, since these effective flyers will complete less stopovers, and therefore be less in tune with the environmental conditions at the breeding ground compared to species which complete numerous stopovers on route (Møller, Rubolini and Saino, 2017). These interspecific differences emerging between advancement trend consequently mean that certain species are more vulnerable to phenological mismatch and population decline. Furthermore, Ockendon et al. (2012) explored the effects of overwintering location on UK migratory birds. They categorised house martins and willow warblers as overwintering in 'Humid Zones', whereas swallows and swifts in 'Southern Zones'. They reported that birds from humid zones exhibited weaker population declines (–2.95% per year) compared to species in southern zones (–3.82% per year), aligning with the finding that larger population sizes correlate to improved phenological synchronisation.

Swallow

Swallows exhibited the greatest arrival advancement rate over the study period, advancing by 2.13 days decade^{-1}. This trend aligns with a previous analysis which found swallows to have one of the greatest advancement trends of all common migratory birds breeding in the UK, exhibiting an arrival 14.8 days earlier in the 2000s than the 1960s (Newton et al., 2006). Similar trends have been observed across Europe, including breeding grounds in Spain, Denmark and Italy (Gordo, 2007; Balbontín et al., 2009). The findings of this study and corresponding previous analyses suggest that swallows are adjusting migration timing possibly in attempts to match timing with optimal resource abundance at breeding sites. However, the divergence index exhibited in this study of -0.05 per year (p=0.2) could result in swallows arriving earlier than spring onset if advancement continues at this rate, and risking fitness through reduced alignment with peak insect abundance. Complexities arise when considering the mechanisms driving swallow advancement. One theory for their advancement is the effect of a large population size, reported as 705,000 breeding pairs in the UK(BTO, 2015b). Newson et al. (2006) reported a strong positive correlation between swallow abundance and earlier arrival time, supporting the strong correlation between arrival time and population size evidenced by Tryjanowski and Sparks (2001). Another theory is the effect of the positive temperature-arrival correlation in swallows (Huin and Sparks 1998), with Sparks (1999) reporting an arrival advancement of 1.6–1.8 days per 1ºC increase in temperature. The climatic conditions at the overwintering site have also demonstrated strong influence over arrival timing, albeit with less evidence. These external factors control individual body condition at departure (Gordo, 2007) and lead to intraspecific variance in departure timing between individuals (Balbontín et al., 2009). In this study, only 7% of interannual variance in swallow arrival was attributed to spring onset, indicating that swallow advancement has not effectively matched with spring phenology in the breeding ground over this study period. More research is required on climatic conditions at overwintering grounds and along migration routes to determine the mechanisms driving swallows' continental-scale advancement and to assess the extent to which their continued earlier arrival risks mismatch with peak insect abundance.

Swift

Conversely, swifts exhibited a delayed arrival rate of 1.6 days decade^{-1} over the study period. This finding corresponds with Newton et al.'s (2006) migration analysis which found swifts to have one of the least pronounced arrival advancements among 14 UK migratory bird species, arriving only 4.7 days earlier in the 2000s compared to the 1960s. These findings highlight the species' limited phenotypic plasticity and ineffective alignment with spring phenology in the UK compared to the other migratory species in this study. Swifts exhibited a divergence index trend of 0.07 per year ($p=0.08$), suggesting increasing levels of phenological mismatch over the study period. This trend aligns with trends of rapid population decline in swifts, with numbers declining by 66% between 1995-2022 to just 59,000 breeding pairs – approximately 90% lower than the UK swallow population (BTO, 2014). Furthermore, this study attributed 1% of interannual variance in swift arrival to spring onset, reflecting very little evidence of interannual matching between swift arrival timing and spring phenology. These findings indicate that swifts should be prioritised for conservation efforts due to their high risk of phenological mismatch, driven by inflexible phenotypic plasticity, a declining population size and worsening climatic conditions.

House martin and willow warbler

House martins and willow warblers exhibited minimal changes in arrival advancement rates over the study period, advancing by just 0.34 and 0.92 days decade^{-1} respectively, demonstrating effective synchronisation with spring phenology and peak resource availability. Both species exhibited minor divergence trends over the study period, with house martins increasing by 0.01 per year (p=0.77), and willow warblers declining by -0.01 per year (p=0.69). These trends indicate that both species have effectively synchronised arrival timing with shifting spring phenology over the study period. This ability to better match spring phenology may be influenced by their further north overwintering locations (fig.2) and larger population sizes, aligning with the finding that larger population sizes correlate to improved phenological synchronisation (Tryjanowski and Sparks, 2001). This was demonstrated in this study by willow warblers with the largest population size of 2.3 million breeding pairs (BTO, 2015c), and the greatest correlation with spring phenology, with the SI accounting for 47% of the variance in arrival timing (p<0.001). This species has shown the most effective synchronisation with shifting spring phenology, likely driven by their large population size in line with the strong correlation between arrival time and population size evidenced by Tryjanowski and Sparks (2001). The species' effective adaption to changing conditions is further supported by Remisiewicz and Underhill (2020) who attributed 59% of interannual variation in willow warbler arrival to climatic drivers controlling spring onset, highlighting the species' ability to modify migration based on previously faced ecological conditions.

4.5. Wider implications and future research

The findings of this study highlight the immediate impacts of anthropogenic climate change on spring phenology, with advancing spring onset strongly correlated with temperature. However, mismatch in advancement rates has been evidenced, aligning with previous evidence of higher trophic levels exhibiting less pronounced advancements than lower trophic levels (Thackeray et al., 2010; Thackeray et al., 2016). Furthermore, clear intraspecific variance in avian species ability to track changes in spring phenology has been detected. Whilst most of these findings were statistically insignificant, the magnitude and direction of the trends provide crucial insight into emerging phenological mismatch. Avian species experiencing greater divergence in arrival timing relative to spring onset are at greater risk of mistiming breeding with peak resource abundance, likely resulting in reduced reproductive success and subsequent population decline (Saino et al., 2010; Visser and Gienapp, 2019). Climate-driven phenological mismatch caused 43.8% of bird extirpation globally in the 20th century, ranging to 51.4% in tropical species (Wiens, 2016). It is likely that a positive feedback loop is establishing, as declining population sizes intensify mistimed migrations, largely driven by anthropogenic climate change and in particular rising temperature. Declining avian populations are having wider ecosystem impacts. Mayor et al. (2017) reported disruptions to the top-down control of insect populations, and subsequent insect outbreaks and increased tree defoliation. Furthermore, Matthews et al. (2024) found these disruptions could increase human disease outbreaks due to the reduction in avian predation on disease vectors.

From this study, a key knowledge gap has been identified regarding the optimal timing of bird arrival for fitness. Without this understanding, accurately assessing the consequences of phenological mismatch remains difficult, as certain species might unexpectantly benefit from mismatched arrival under certain environmental conditions. Further research is required to determine the conditions that maximise reproductive success for individual species, as well as the degree to which arrival timing influences fitness. Furthermore, more comprehensive demographic data from increased bird ringing and GPS tracking of migration routes is required to accurately report population change. Finally, additional data on climatic conditions and habitat loss via land-use change in overwintering locations is needed to establish more in depth analyses into the mechanisms driving shifts in avian phenology, following the recent study by Finch et al. (2022) finding that increased precipitation was causing higher nest failure, smaller brood size and lower first year survival.

5. Conclusions

This study has proven clear interspecific variation in avian species' ability to match arrival timing to spring phenology in the UK from 2000-2021. Whilst many of the results lacked statistical significance, the size and direction of phenological effects are still of crucial importance for future implantation of conservation efforts.

Spring phenology of the Angiosperm and Insecta classes in this study exhibited no statistically significant trends, however the majority did display advancing phenological shifts at varying magnitudes. These advancing tendencies align with previous metanalyses conducted at larger scales and over longer time periods. Furthermore, the SI was strongly correlated with spring temperature, highlighting the effectiveness of spring phenology as an indicator of climate change. Therefore, it is highly likely that the lack of significant spring phenology trends can be attributed to the stabilisation of average spring temperature over the study period.

Within the Aves class, willow warblers emerged as the most adaptive species, demonstrating strong and consistent alignment with the SI both year-to-year and long term. House martins also exhibited relatively successful synchronisation with spring phenology. Conversely, swallows exhibited potential for increasing mismatch from earlier arrival, while swifts exhibited delayed arrival trends and a long-term divergence from spring events. These results suggest that swifts require the most urgent conservation efforts.

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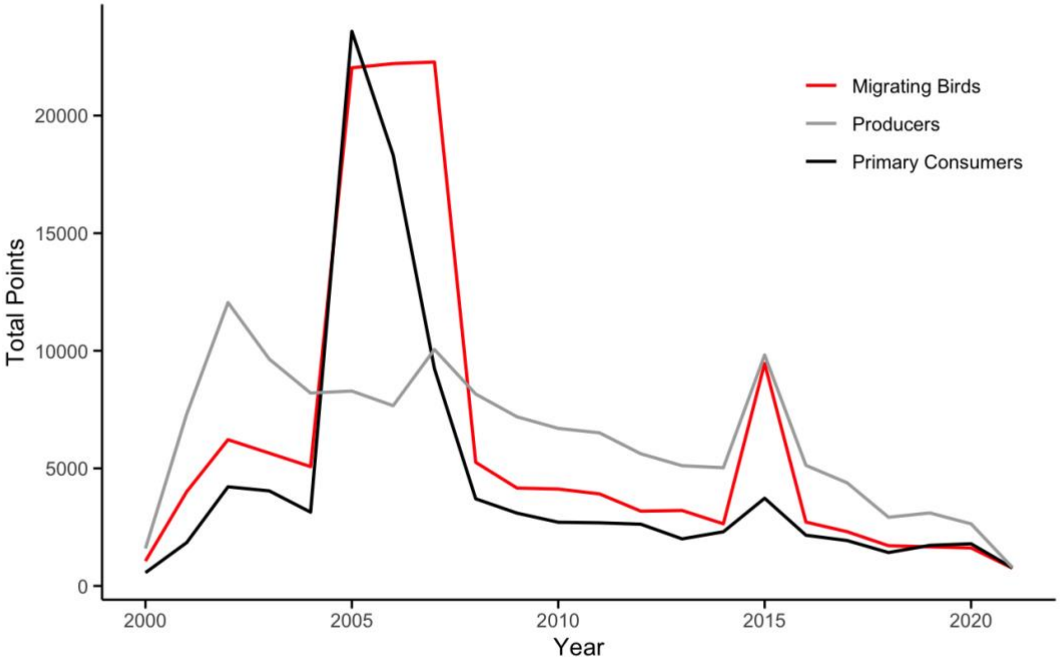
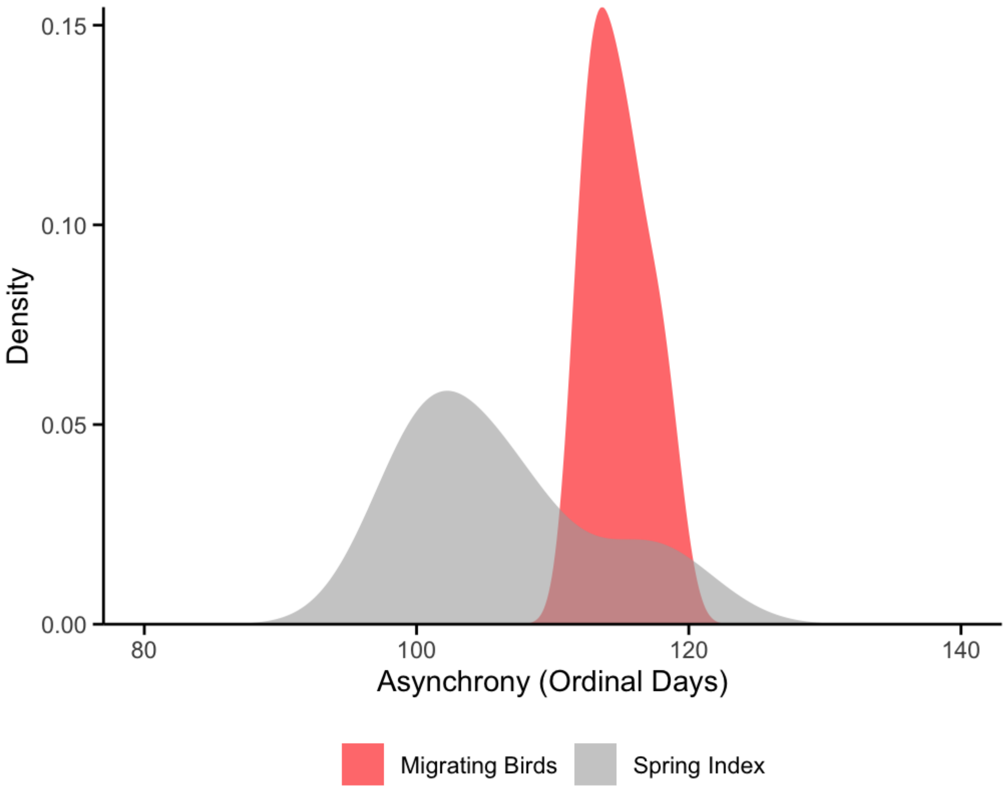
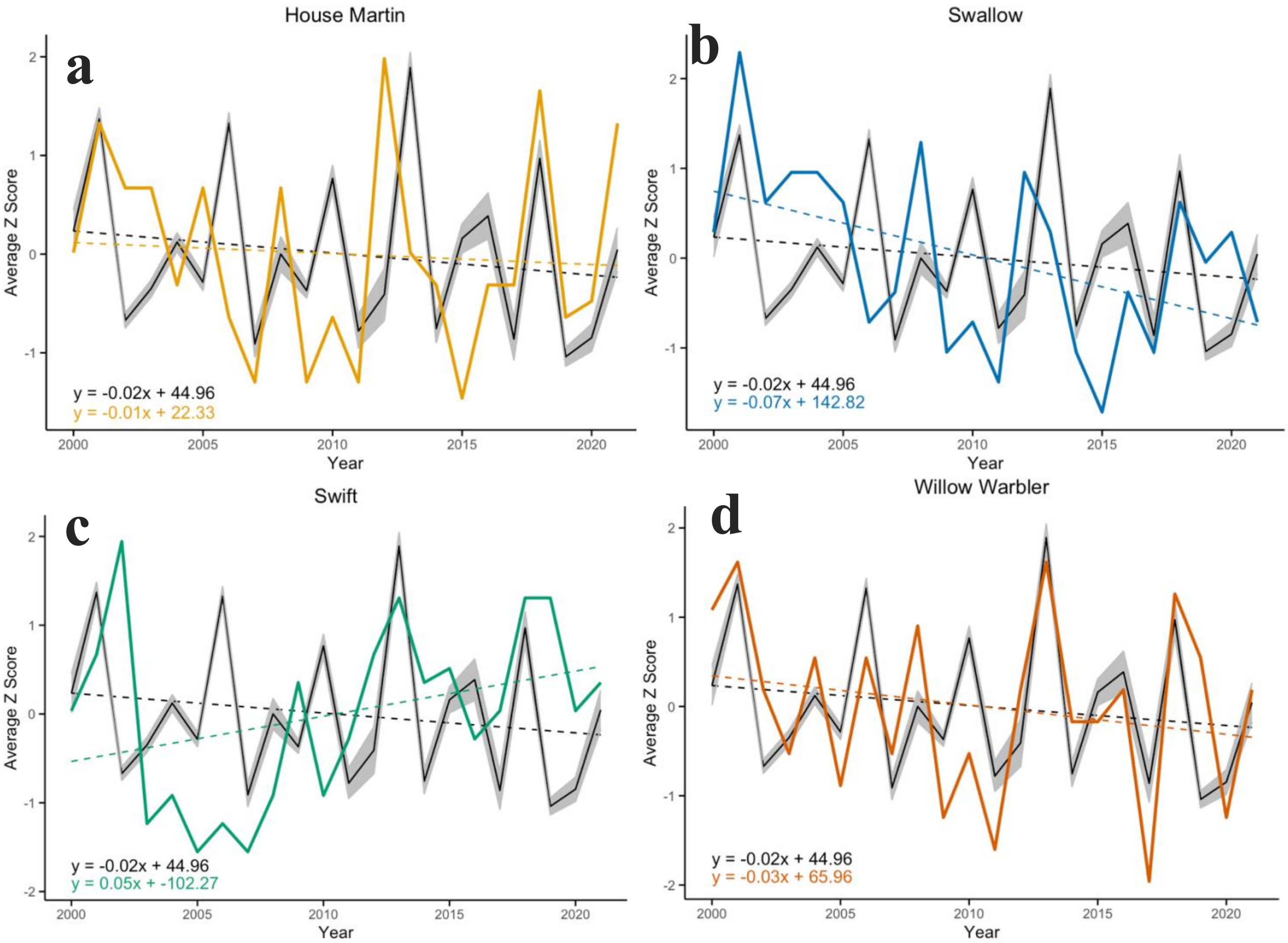
Appendices



Appendix 1. Temporal variance in number of datapoints for each taxonomic group. Red line: Aves class, grey line: Angiosperm class, and black line: Insecta class.



Appendix 2. Density distribution of all migratory bird arrival DOY data against SI onset DOY data



Appendix 3. time-series analyses of migratory bird arrival and SI. a) house martin, b) swallow, c) swift and d) willow warbler