Developing a national indicator of functional connectivity

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ABSTRACT

Habitat loss is a significant driver of biodiversity loss, causing fragmentation into small, isolated patches of suitable land cover. This reduces the permeability of landscapes to the movement of individuals and reduces the likelihood of metapopulation persistence. Quantifying functional connectivity, the ability of a focal species to move between resource patches, is therefore essential for conservation management. There is substantial evidence supporting a technique based on 'population synchrony'- the degree of correlation in time-series of annual population growth rates between different long-term monitoring sites, to provide a measure of functional connectivity. However, synchronised population dynamics are not only driven by the movement of individuals between sites, but also shared environmental conditions which must be accounted for. Here, we use species survey data from over four decades to investigate average levels and temporal trends in population synchrony for 58 British bird and butterfly species. We first show that population synchrony is significantly associated with synchrony in some seasonal climatic variables. Once we accounted for spatiotemporal climatic patterns, we found that synchrony in butterflies declined over time by 71% between 1985 and 2000 but increased by 64% in recent years. Synchrony in birds showed some decline between 1999 and 2005, after which there appears to being recovery, however most species (74%) show no significant overall change in synchrony. Our proposed indicator provides a 'species-eye-view' of functional connectivity using widely available abundance data. Developing such indicators of functional connectivity, which can be updated annually, is crucial to improve the effectiveness of land management strategies for conservation under increasing environmental change.

1. Introduction

Habitat loss and fragmentation is a key concern of conservation policy both in the UK and globally, as it is implicated as the main driver of biodiversity loss in numerous taxa across a variety of regions (Butchart et al., 2010; Fahrig, 2003; Pimm et al., 2014). Despite decades of conservation action, the Convention on Biological Diversity (CBD) Aichi Target 12 has not achieved its target to halt species extinctions or reverse declines (Buchanan et al., 2020). Habitat fragmentation, driven by anthropogenic land-use change, decreases the amount of available habitat and increases ecological isolation between patches. This can result in an increased extinction risk and a reduction in the exchange of individuals among fragmented populations (Hanski, 1998). Therefore, functional connectivity, i.e. the ability of individuals and populations to move between resource patches in response to landscape elements, is crucial for managing and conserving viable metapopulations (Hanski, 1998; Tischendorf and Fahrig, 2000). Dispersal across landscapes is also essential for range expansion under climate change and the maintenance of genetic diversity (Hanski, 1998; Hanski and Gilpin, 1991).

Measuring levels of functional connectivity is vital for monitoring and predicting the effects of climate change and increasing habitat fragmentation on population persistence. Traditional approaches to calculate functional connectivity have focussed on measuring dispersal. Empirical movement data has been collected using mark-release-

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recapture (MRR) methods (Roland et al., 2000; Sutcliffe et al., 2003, 1997), by radio-tracking individuals (Rubenstein and Hobson, 2004; Sutcliffe and Thomas, 1996), or more recently, by using landscape genetics to measure the genetic similarity of populations (Clegg et al., 2003; Fenderson et al., 2020; Schwartz et al., 2002). However, these techniques are expensive, time consuming and labour intensive, and can therefore only be carried out over small spatial scales and/or short time periods (e.g. Finch et al., 2020). Other models of functional connectivity are mechanistic and built from sound theoretical understanding of dispersal capabilities (e.g. Watts & Handley 2010; Bocedi et al. 2014; Merrick & Koprowski 2017), but are rarely validated using empirical data (Laliberté and St-Laurent, 2020). For example, a previous indicator of functional connectivity for the UK used metrics based on land cover combined with expert opinion of species' habitat associations and movement capacity (Watts and Handley, 2010). This approach has limitations in that land cover data are not updated frequently and there is substantial uncertainty in estimating species' movement capacities across different land cover types (Watts et al., 2008). It is therefore ideal for indicators of functional connectivity to be data-driven and assessed from a species' point of view to robustly inform conservation policy.

An alternative method to estimate functional connectivity has been proposed based on a measure of population synchrony — the correlations in time series of annual population growth rates between different locations — using long-term species monitoring data (Oliver et al., 2017; Powney et al., 2012, 2011). This is because the movement of individuals between sites is known to lead to increased synchrony in population dynamics (Hanski 1998; e.g. Ranta et al. 2008). Density-dependent emigration of individuals can link populations, leading to increased levels of population synchrony (Fig. 1). Empirical evidence has shown that population dynamics in different locations are more synchronised for species with high estimated dispersal ability, as measured using mark-release-recapture (Paradis et al. 1999; Bellamy et al. 2003), expert

opinion (Sutcliffe et al. 1996), or using dispersal-related traits as a proxy for dispersal ability (Tittler et al. 2009). Additional research has found correlations between population synchrony and landscape suitability (Powney et al., 2012, 2011), demonstrating the sensitivity of population synchrony to the movement of individuals.

However, population synchrony can also be driven by shared environmental conditions, i.e. the 'Moran effect' (Koenig, 2002; Moran, 1953), which declines with increasing distance between populations, partly due to spatial autocorrelation in climatic conditions (Hanski and Woiwod, 1993; Powney et al., 2011; Roland and Matter, 2007). Additional research has shown that populations are more synchronised if they occupy similar habitat types (Powney et al., 2011, 2010) or are situated at geographic range margins (Mills et al., 2017; Powney et al., 2010), potentially driven by increased climatic constraints on marginal populations reducing the availability of suitable microhabitats (Oliver et al., 2014; Powney et al., 2010). To explain changes in population synchrony over time, several studies have concluded that climate is a major driver of temporal trends (Sheppard et al. 2016; Shestakova et al. 2016; Black et al. 2018; Dallas et al. 2020; but see Cayuela et al. 2020). For example, climate change could be driving an increased frequency of extreme weather events, leading to greater synchronised population dynamics (Black et al., 2018). In addition, there may be temporal trends in the degree of spatial autocorrelation in climate (Post and Forchhammer, 2004).

To obtain a better signal of dispersal, one would need to account for the Moran effect in estimates of population synchrony. After accounting for relevant climate-related factors (including distance between sites, habitat similarity, shared climate, and position in geographic range), recent evidence has shown that residual synchrony reflects actual movements of individuals measured using mark-release-recapture (Oliver et al., 2017). Thus, evidence is accumulating to suggest that, if climate can be sufficiently taken into account, the movement of individuals has a key role in promoting population synchrony in population dynamics across space (Oliver et al., 2017).

To further develop and operationalise the use of population synchrony as an indicator of functional connectivity, we calculate temporal trends in population synchrony for 58 British birds and butterflies using long-term monitoring datasets from 1980 to 2016 for a total of 3,306 sites across Great Britain. We use data from three monitoring schemes: the UK Butterfly Monitoring Scheme (UKBMS), the Common Birds Census (hereafter CBC), and the Breeding Bird Survey (hereafter BBS). We develop new approaches to account for spatiotemporal climatic patterns that drive correlated population dynamics, i.e. a dynamic Moran effect. After accounting for these effects of climate, we produce a residual temporal trend in population synchrony that reveals changes in functional connectivity over time.

2. Methods

2.1. Data collation

Butterfly data were derived from the United Kingdom Butterfly Monitoring Scheme (UKBMS) (Pollard and Yates, 1993). UKBMS transects are walked by trained volunteers who survey 5 m-wide strip transects for 26 weeks between April and September recording all butterflies observed. Further details can be found in Pollard and Yates (1993) and in Rothery and Roy (2001). An index of abundance for each butterfly species for each transect, each year from 1980 to 2016, was extracted from the UKBMS database. To ensure adequate data for analysis, resident butterfly species which had at least 75% of years with 50 sites or more sampled per year were included in the analysis.

We focussed our functional connectivity indicator on species included in the Defra woodland bird indicator (Defra, 2020b), therefore we derived woodland bird abundance data from two datasets, the Common Birds Census (CBC) and the Breeding Bird Survey (BBS). The CBC monitoring scheme monitored population trends for British
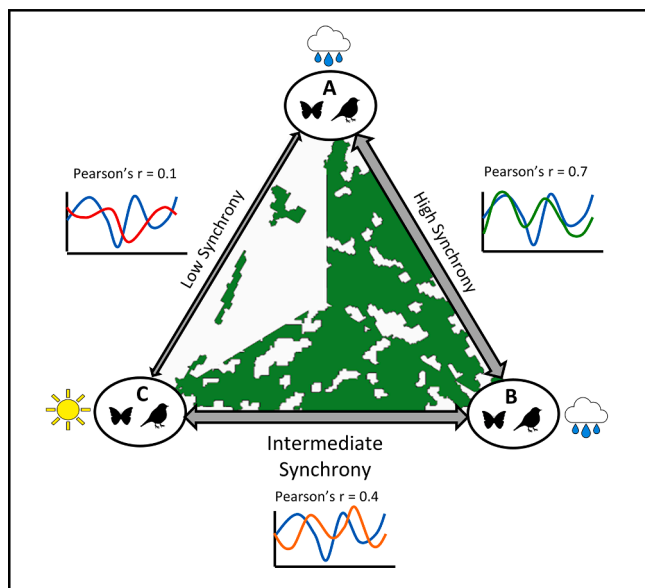

Fig. 1. Schematic of factors which influence population synchrony. Sites A and B share the same climate and have a highly permeable landscape matrix between them (green shaded areas), allowing greater movement of individuals. These sites therefore have high synchrony. Sites B and C also have movement of individuals, but do not share the same climate, and have intermediate levels of synchrony. Finally, sites A and C have different climatic conditions and the hostile matrix of habitat prevents movement of individuals. Therefore, these sites have low levels of synchrony. Pearson's r values were chosen to reflect synchrony values for high, low, and intermediate synchrony. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

breeding birds from 1962 until 2000 (Marchant, 1990). Volunteer observers undertook repeated surveys between 8 and 10 times a year between late March and early July, recording all species seen or heard at each site. The BBS has monitored birds since 1994, where two 1 km transects are visited twice a year, once between April and mid-May (early visit), and once between mid-May and the end of June (late visit) and all birds seen or heard are recorded (Harris et al., 2018). The total number of adult birds of each species for each site and each visit are calculated for each year. We obtained the maximum number of adult birds across all visits at each site for the years 1980–2000 from the CBC and 1994–2016 from the BBS. Species which had at least 75% of years with 50 sites or more sampled per year were included in the analysis.

In addition to interannual fluctuations in population size, raw abundance values also reflect long-term temporal trends arising from drivers such as land use and climate change, therefore we used between-year rates of change to focus on interannual population synchrony (Bjørnstad et al., 1999). We converted annual abundance values into rate of change as follows: $logN_t – logN_{t-1}$, where N_t is the abundance index estimate in time t (Powney et al., 2010). We added one to all population counts prior to the growth rate calculation to avoid taking the log of zero.

2.2. Population synchrony

For each species, population synchrony between all pairs of monitoring sites was estimated as the Pearson's correlation coefficient of yearly population growth rates. To assess temporal trends in population synchrony, we repeatedly calculated population synchrony using a 10-year moving window (Bjørnstad et al., 1999). A 10-year moving window was selected to balance the need for a reasonable-length time series to estimate population synchrony versus the number of separate windows where we could calculate population synchrony. The following pair-wise site combinations were excluded from the analysis: i) for either site, <7 years of growth rates in common to ensure data quality, ii) for either site with a chain of zero abundance counts followed by positive values (associated with new site colonisation), as this can inflate synchrony values and increase Type I errors, and iii) site combinations that were more than 100 km apart. Although evidence has shown synchrony remains positively associated with landscape suitability for sites up to 200 km apart (Powney et al., 2011), we selected an upper distance limit of 100 km for computational feasibility. Additionally, due to computational limitations, synchrony was only calculated on BBS sites with at least 10 years of data, and a maximum of 10,000 random pairs of sites. This represents a subset of sites for species with large amounts of data (ranging from 3% to 98% of total available site comparisons with a median of 14%). We repeated this process five times to confirm that each subset adequately represented the whole dataset (Figure A2). The resulting dataset had population synchrony values for 32 butterfly species from 701 sites between 1980 and 2016, 26 bird species from 106 sites between 1980 and 2000, and 24 bird species from 2,499 sites between 1994 and 2016 (Table A1-A3).

2.3. Climate synchrony

To determine whether temporal trends in population synchrony are driven by patterns in climatic synchrony over time, we measured synchrony of mean temperature and mean precipitation for each season (spring, summer, autumn and winter for mean temperature and mean precipitation) using 5 km gridded climate data (Met Office et al., 2017). We converted coordinates from the sites where we measured species population synchrony from 1 km to 5 km grid squares and matched these to climate data for each of the three datasets. Climate synchrony was calculated using the same method as population synchrony, i.e. calculating a Pearson's correlation metric for each climate variable between each pair of monitoring sites for grid squares using a 10-year moving window. The resulting dataset had climate synchrony values for 4

seasons from 686 UKBMS sites from 1980 to 2016, 106 CBC sites from 1980 to 2000 and 2490 BBS sites from 1994 to 2016 (Figure A1). Samples sizes are very slightly lower due to a small number of species monitoring sites with no climate data.

2.4. Additional control variables

To control for other known drivers of population synchrony, three attributes were calculated for each pair of sites, in each dataset. First, distance was calculated as the Euclidean distance (km) between each pair of sites. Second, northerliness was calculated as the mean Northing (km from Ordnance Survey National Grid) between each pair of sites. Finally, we used a Renkonen's percentage similarity index to calculate habitat similarity of a 500 m buffer surrounding each focal pair of sites (Jost et al., 2011; Renkonen, 1938). The index was bound between 0 and 1, with a value of 1 for two sites surrounded by the same habitat composition, and 0 being completely distinct compositions. Habitat data were extracted from the CEH Land Cover Map 2007 (Morton et al., 2011) and aggregated to the broad habitat level (10 habitat biotopes in total). This landcover map represents a roughly intermediate point in our indicator time series, and UK biotopes have not changed commonly or substantially enough for there to be frequent substantial differences in habitat composition between maps (plus, there are issues with comparability between maps due to changes in remote sensing and processing methodology) (Carey et al., 2008). Sites for CBC were primarily woodland sites with woodland type recorded by trained volunteers as a categorical variable (four types), therefore habitat similarity was calculated as a binary variable, with 1 representing a pair of sites with the same woodland type and 0 representing a pair of sites with different woodland types.

2.5. Trends in abundance

Changes in synchrony over time could be reflected in changes in abundance due to 'propagule pressure' (emigration of individuals) of highly abundant species facilitating the spread of populations, and therefore increasing population synchrony. To investigate this, we calculated the change in abundance for butterflies, using the UKBMS Collated Index data which is a national annual index for each species for each year derived using a statistical model (Moss and Pollard, 1993; Rothery and Roy 2001). We compared mean abundance using a t-test between two independent 10-year windows: 1980–1989 and 1995–2004, representing the change in abundance for the first two decades, and between 1995 and 2004 and 2007–2016 for the latter two decades for each species. For birds, we used the joint CBC/BBS population trend data to compare mean abundance using a t-test between 1980 and 1989 and 1991–2000, representing the time period of change for CBC data, and between 1994 and 2003 and 2007–2016, representing the time period of change for BBS data. Each species was classified as either increasing, decreasing, or showing no change in abundance over time.

2.6. Statistical analysis

All statistical analysis was carried out using R 3.5.0 (R Core Team, 2018).

2.6.1. Accounting for climatic synchrony

We first sought to account for variation in population synchrony that could be attributed to climate synchrony, not to infer which climate variables were important. We found no evidence for collinearity between each climate synchrony variable for each dataset. We fitted a mixed effects model using the *lme4* package (Bates et al., 2015) to each of the three monitoring datasets separately ('all species models'). Each model contained population synchrony values for every pair-wise site comparison for each species as the response variable, the mid-year of

each moving window as a categorical fixed effect, and each of the eight climate synchrony variables as continuous fixed effects. Species and pair ID of the sites were included as random intercepts to account for repeated measures and the number and identity of monitoring sites varying through time. Any climate variable with a significant relationship with population synchrony ($p < 0.05$) was included as a covariate in future analyses to account for climatic effects. We note that this approach could be conservative as we may be less likely to detect other patterns in population synchrony than if we had attempted to avoid any possible overfitting.

Secondly, we investigated for evidence of increasing variance in climate over time over the study period. We used an F-test to determine whether the variation in seasonal mean temperature and total precipitation for each season differed between 1985 and 2000 and 2000–2012.

2.6.2. Temporal trends in population synchrony

To estimate a temporal trend in population synchrony for all bird and all butterfly species, while accounting for known drivers of synchrony, we ran modified versions of the 'all species models' for each dataset by including distance, habitat similarity, mean northerliness, and the significant climate synchrony variable (unique for each dataset) as continuous fixed effects. All fixed effects were standardised to zero mean and one standard deviation. The coefficients for each mid-year and their associated standard errors were extracted from the model and are used as our index of population synchrony and associated uncertainty for each 10-year moving window. Population synchrony values for the first year were standardised at 100.

To assess how individual species were changing in population synchrony over time, we refitted the mixed effects model for each species within each dataset separately ('single-species models'). We used only two mid-year values as fixed categorical effects which were chosen to ensure there was no overlap in the 10-year moving window (i.e. they represent independent input data) and to match the time periods for species change in abundance. For butterflies, we examined change between two 10-year periods with mid-years of 1985 and 2000, and subsequently between two 10-year periods with mid-years of 2000 and 2012. For CBC birds we examined change between two 10-year periods with mid-years of 1985 and 1996 and for BBS birds between two 10-year time periods with mid-years of 1999 and 2012. For each species, the coefficients and associated p-values for each mid-year were extracted to determine whether each species had experienced an increase or decrease in population synchrony between the two comparison periods. Some species had insufficient data for the mixed effects model to run and could not be analysed individually (Table A1 & A2). Since synchrony measures of pair-wise sites are not independent, to obtain p-values we ran 1,000 permutation tests (e.g. see Powney et al. 2012) on each species to determine the significance of change in synchrony between the two comparison years. At each permutation, the predictor variable (year) was randomised, and a linear mixed effects model fitted, and the F-values extracted. We plotted the frequency distribution of the F-values and calculated the p-values for each predictor variable based on the position of the observed vs. simulated values (e.g. a value in the top 5% of the F-value frequency distribution would have a significant p-value of < 0.05).

All models are described using mathematical notation in Supplementary Material Appendix B.

2.6.3. Trends in abundance and population synchrony

To determine whether changes in population synchrony over time are explained by trends in abundance, we used chi-squared tests to test for a significant association between the change in synchrony and change in the three abundance categories (i.e. significantly increasing, significantly decreasing or no change) over time as calculated in the 'Trends in abundance' section above.

3. Results

3.1. Climate accounts for variation in population synchrony

We selected which climate synchrony variables explained a significant amount of variation in population synchrony for each dataset. For UKBMS, we selected all eight climate synchrony variables ($R^2 = 0.00035$) (Table A4). For CBC birds, only summer temperature was included ($R^2 = 0.00024$) and for BBS birds, spring, autumn, and winter rainfall were selected ($R^2 = 0.000014$) (Table A4). These variables were included in all future models as fixed effects to account for the relationship between climate and population synchrony. We found no significant results to suggest that variation in seasonal mean temperature and rainfall has differed between 1985 and 2000 and 2000–2012 (Table A5).

3.2. Overall trends in population synchrony for birds and butterflies

Population synchrony in butterflies ranges between -1 and $+1$ with a median value of 0.3. The temporal trend in population synchrony for butterflies declined until 2004, thereafter it rapidly increased (Fig. 2a). This trend was reflected across the 32 butterfly species studied, with 71% of species declining in synchrony between 1985 and 2000, and 64% increasing in synchrony between 2000 and 2012 (Fig. 2d). Population synchrony in birds also ranges between $+1$ and -1, with a median value of 0.03 for CBC birds and 0.1 for BBS birds. Synchrony in birds was stable between 1985 and 1996 (Fig. 2b) with most species (74%) showing no trend in synchrony. Although synchrony values look identical between 1985 and 1996, there is variation in synchrony from 99.6 to 100.4. From 1999 onwards, birds declined in synchrony until 2005 where they appeared to be showing some signs of recovery (Fig. 2c). However, 74% of species showed no change in synchrony between 1999 and 2012 (Fig. 2e).

3.3. Control variables affecting population synchrony

For all three control variables in our mixed effects model, our results followed the general expectations based on previous evidence. We found that more northerly pairs of sites, those closer together and those with similar habitat types had higher levels of population synchrony (Fig. 3). For birds, we found only BBS sites which have similar habitat type to have higher average synchrony (Fig. 3). These results remained significant after running 1,000 permutation tests (Table A6).

3.4. Trends in abundance and population synchrony

We found no significant association between the categories of abundance change and population synchrony change for butterflies between 1985 and 2000 $\chi^2 = 2.92$, P = 0.47) and between 2000 and 2012 ($\chi^2 = 5.90$P = 0.19), and for CBC birds ($\chi^2 = 2.51$P = 0.81), and BBS birds ($\chi^2 = 1.7$P = 0.80).

4. Discussion

The proposed indicator presented, based on a population synchrony, offers a 'species-eyed-view' of functional connectivity using a data-derived method based on widely available, annually updated species monitoring data. We found patterns in population synchrony clearly associated with synchrony in temperature and rainfall. Once these variables were accounted for, we demonstrated temporal trends in residual population synchrony for UK birds and butterflies, suggesting that functional connectivity is changing over time.

Successful biodiversity indicators summarise complex ecological datasets into robust measures that can be used to assess trends over time and are used to assess progress towards meeting national and international goals and targets and help inform governmental policy (Butchart
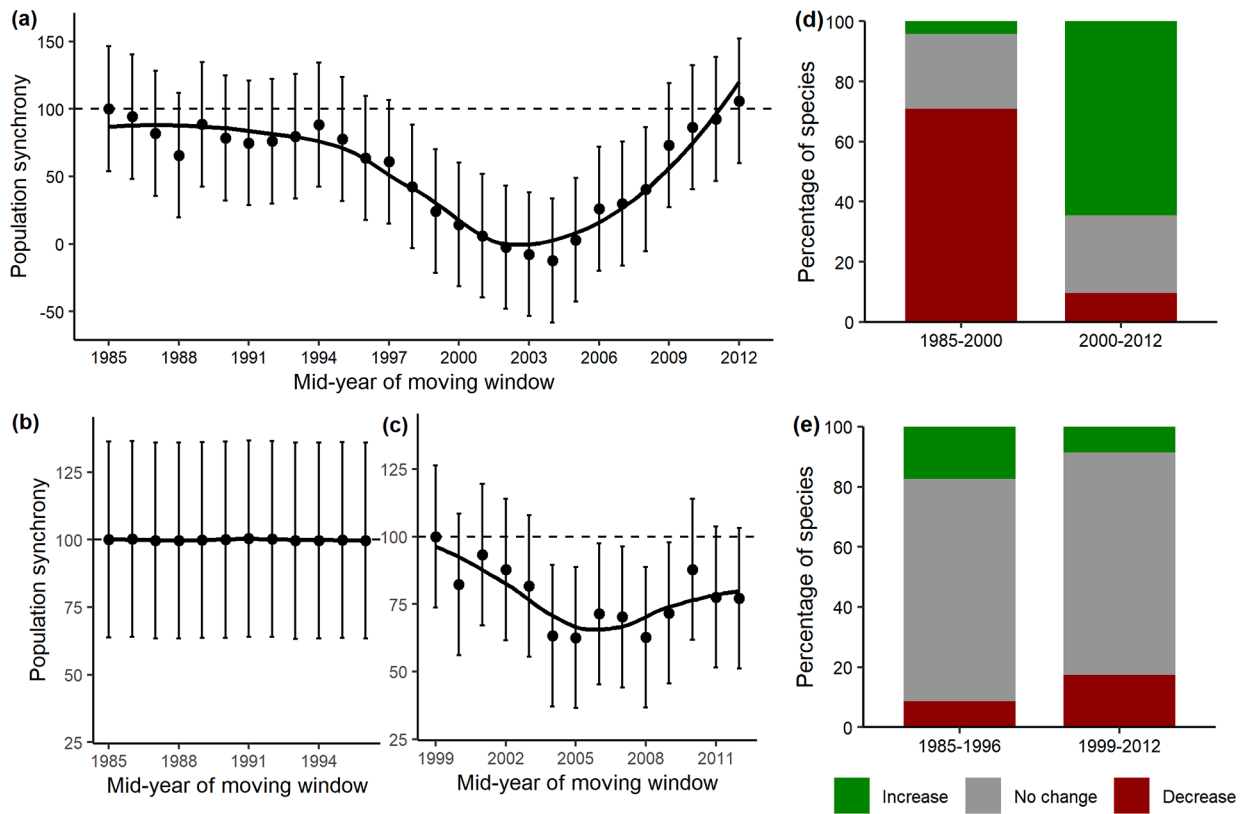
Fig. 2. The temporal trend in population synchrony fitted using a LOESS regression function with standard error bars for (a) butterflies between 1985 and 2012, (b) CBC birds between 1985 and 1996, and (c) BBS birds between 1999 and 2012. Population synchrony scores were standardised, so the first mid-year was set to 100. Bar charts show the percentage of species which have either statistically significantly increased, decreased or remain unchanged in population synchrony between (d) 1985–2000 and 2000–2012 for butterflies (n = 24 and n = 31 species respectively) and (e) 1985–1996 for CBC (n = 23 species) and 1999–2012 for BBS (n = 23 species).
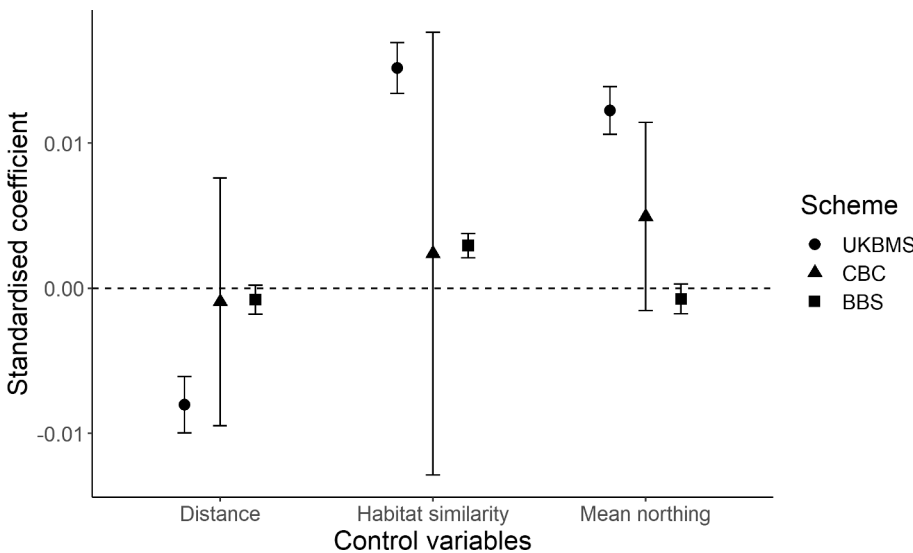

Fig. 3. Standardised regression coefficients from mixed effects models with average synchrony as the response variable and control variables as fixed effects. Symbols mark the regression coefficients for each fixed effect and error bars mark the 95% confidence intervals. A positive coefficient indicates that a higher level of a given control variable (i.e. greater distance, greater habitat similarity and higher mean northing) is associated with greater synchrony in population dynamics between sites for that species.

et al., 2010; Costelloe et al., 2016; McQuatters-Gollop et al., 2019). Developing an indicator of functional connectivity involves a trade-off between the data requirements and level of information produced (Calabrese and Fagan, 2004). Basic measures of structural connectivity, for example average nearest neighbour distances of biotope types deemed suitable habitat, do not require extensive data, but they only produce a simple estimate of connectivity that, for example, ignores the differing resistance of intermediate landcover types (Watts and Handley, 2010). Complex mechanistic models can produce very detailed estimates of connectivity (e.g. Watts & Handley 2010; Bocedi et al. 2014; Merrick & Koprowski 2017), but are very data intensive and require validation from independently collected data (Laliberté and St-Laurent, 2020). Similarly, direct observations of species' movements, for example from mark-release-recapture, provide more realistic estimates of connectivity but are very data-intensive and often limited to small spatial scales (Calabrese and Fagan, 2004).

Our proposed indicator utilises widely available abundance data to calculate a temporal trend in population synchrony, which may provide an estimate of connectivity. Empirical evidence has shown correlations between population synchrony and the distance by which populations were separated by hostile land cover types (Roland and Matter, 2007) and the coverage of quality habitat types in the intervening landscapes (Powney et al., 2011). Furthermore, the distance along woodland edges has shown to be a better predictor of local synchrony and species movement (measured using mark-release-recapture) than Euclidean distance (Powney et al., 2012; Sutcliffe and Thomas, 1996). Additionally, higher population synchrony has been found between patches with higher frequency of movements between them, obtained from mark-release-recapture of a butterfly species (Oliver et al., 2017). This empirical evidence demonstrates that population synchrony does reflect movement frequencies rather than being solely driven by shared climatic conditions or connectivity of interacting species.

However, if we seek to track connectivity using population synchrony, we need to account for climate as a confounding variable. Previous research has shown parallel increases in population synchrony and environmental synchrony, suggesting a potential role of the Moran effect in driving shared population dynamics over time (Kahilainen et al., 2018; Koenig and Liebhold, 2016; Sheppard et al., 2016; Shestakova et al., 2016). Here, we show that population synchrony is significantly associated with synchrony in some seasonal climatic variables. For butterflies, each of the eight climate variables tested were individually associated with population synchrony, whereas for the BBS dataset, only three rainfall variables were significant and for CBC birds only summer temperature (Table A4). This provides convincing evidence that synchrony in temperature and rainfall play a role in driving shared population dynamics (Koenig, 2002; Koenig and Liebhold, 2016; Post and Forchhammer, 2004; Sheppard et al., 2016). Our results also confirm that sites which are closer together, share similar habitat, and are situated closer to species' range margin have higher mean synchrony values (Powney et al., 2010; Roland and Matter, 2007; Sutcliffe et al., 1996). Increased variation in climate can cause extreme population crashes (Palmer et al., 2017) and drive more synchronised populations (Black et al., 2018; Pomara and Zuckerberg, 2017). However, we found no evidence for significant changes in climate variability over time in our UK dataset (Table A5), suggesting that it is unlikely to be driving trends in shared population dynamics in our current dataset.

Density-dependent emigration can facilitate the spread of individuals (Hanski, 1998). This has been shown to drive more synchronous population dynamics in birds (Bellamy et al., 2003; Paradis et al., 2000, 1999) and butterflies (Roland and Matter, 2007) and could explain the changes in temporal synchrony we find here. However, we found no overall association between the trend in abundance and trend in population synchrony in our three datasets. Despite this, 15 butterfly species (out of 24 species) in our study show a 'u-shaped' pattern in synchrony over time, with a decline between 1985 and 2000 and increase between 2000 and 2012. This suggests that functional connectivity for butterflies may be changing over time in the UK, which could be driven by structural factors in the landscape, for example, geographical barriers and habitat restoration. Many of these species which show a u-shaped pattern in temporal synchrony are wider countryside species and/or associated with garden and hedgerow habitats (Asher et al., 2001) and could be impacted by wider landscape changes. A major push for the uptake of English agri-environment schemes through the Entry and Higher Level Stewardship schemes began in 2005, which is where we also see the inflection point in butterfly functional connectivity trends. The schemes were designed to reduce the negative impacts of agricultural intensification by providing support to farmers for environmentally friendly management (Food and Environment Research Agency, 2013). They led to increased height and width of hedgerows (Food and Environment Research Agency, 2013) and therefore have allowed these habitats to support higher butterfly population densities (Food and Environment Research Agency, 2014). Furthermore,

farms which adopted additional wildlife-friendly management supported 50% higher butterfly species richness compared to farms meeting the minimum requirements (Hardman et al., 2016). Therefore, it is possible that the introduction of agri-environment schemes explains the upturn in butterfly population synchrony/connectivity in the mid-2000 s. In contrast, woodland bird population synchrony remained stable over time, with most species showing no change in synchrony. Woodland cover across the UK has increased from 9% in 1980 to 13.1% in 2018 (in England, this has increased from 7.3% in 1980 to 10% in 2018) (Forestry Commission, 2018). Hence, woodland cover change has not been marked, yet may possibly have contributed to the increase in connectivity for four bird species between 1985 and 1996 and two species between 1999 and 2012. However, woodland cover is low which could explain why synchrony values are lower for birds than for butterflies (e. g. median absolute Pearson correlation values of 0.1, and 0.03 for CBC, and BBS datasets respectively, compared to 0.3 for UKBMS dataset). Although woodland creation has been shown to help recovery of generalist woodland birds, there is often a time-lag of several years while trees mature before species respond to changes in the habitat (Watts et al., 2020). This could explain a more recent recovery in woodland bird connectivity from 2005 onwards. The UK is planning to increase forestry cover substantially by at least 30,000 ha per year under the net-zero 2050 target to reduce carbon emissions (Committee on Climate Change, 2020; Defra, 2020a). Increasing the size and quality of habitat patches can increase the abundance of source populations (Hodgson et al., 2011), which plays an important role in promoting connectivity across the landscape (Robertson et al., 2018) and could lead to further recovery of woodland bird populations.

In addition to changes in landscape structure affecting source population size and improving landscape permeability, functional connectivity might also be explained by changes in individual movement capacity. However, although there is evidence of evolution in movement capacity related to physiological changes (e.g. wing-thorax ratio, see Simmons and Thomas 2004; and Hughes et al. 2007), there is no reported evidence of increased movement capacity over time. In fact, some evidence suggests that at high-latitudes insects may be getting smaller over time (Bowden et al., 2015). Therefore, we anticipate our UK results most likely due to changing structural connectivity related to changes in the landscape character, which could be mediated through habitat management (Hanski, 1998).

Increasing synchrony has been suggested to be a 'double-edged sword', where it is associated with increased extinction risk (Heino et al., 1997). But in practice, absolute levels of symphony are low enough that synchronous extinction seems unlikely (e.g. in our data absolute Pearson correlations have low median values of 0.3, 0.1, and 0.03 for UKBMS, CBC, and BBS datasets respectively). Also, studies considering the association between synchrony and extinction often fail to consider that synchrony is not the driving factor: where populations are highly synchronised (e.g. at range edges; Mills et al. 2017) then weather is the driving factor causing population declines and synchrony is simply the shared response to this driver. Hence, increasing population synchrony arising from enhanced landscape connectivity is unlikely to increase extinction risk, but, instead, can actually make *meta*-populations more robust, as confirmed by substantial theoretical and empirical work (Hanski, 1998).

Our approach of measuring functional connectivity has some limitations. Firstly, measuring cross-correlations between pairs of sites requires a large amount long-term site-based monitoring data to capture the picture of population synchrony across a large spatial scale. To maximise our site data, we included sites which are newly added to the monitoring schemes. However, we included a random effect for site pair ID to account for the identity of monitoring sites varying through time, and therefore allowing utilisation of data from newly added sites. Secondly, although we find evidence that spatial autocorrelation in climate is driving temporal trends in population synchrony, as per previous research (Sheppard et al. 2016; Shestakova et al. 2016; Black et al. 2018;

Dallas et al. 2020), it is possible that there are other climate variables influencing population synchrony which we have not accounted for. For example, previous research has shown that the number of frost nights can cause declines in the population abundance of wrens (Bellamy et al., 2003). However, researchers found the same relationship using mean winter temperature as an explanatory variable, as this measure is highly correlated with the number of frost days. Future analysis could use a species-specific approach tailoring specific climate variables (both type of variable and the time window of measurement) to each species, but we expect it would produce broadly similar results as we have here as it is likely that our seasonal temperature and rainfall variables are correlated with species-specific climate variables.

5. Conclusion

Our proposed indicator based on population synchrony offers a data-driven approach to measuring functional connectivity using widely available abundance data which can be updated annually. Although population synchrony is driven by shared environmental conditions, once accounted for, residual population synchrony has been shown to reflect the movement of individuals. This suggests that the temporal trend in population synchrony can be a useful conservation metric for tracking functional connectivity which can be updated annually. Establishing more long-term and large-scale monitoring schemes for under-recorded taxonomic groups will enable this methodology to be applied to other species groups, such as pollinators. Furthermore, relating fine-scale landscape data to cold- and hot-spots of functional connectivity would allow a greater understanding of what landscape features hinder or promote species' movement between sites. In addition, research linking species' movement capacity with temporal trends in population synchrony would add further evidence to the use of this indicator in facilitating more targeted landscape conservation management.

6. Data availability statement

The data supporting the results (population synchrony scores for every pair of sites for every species for each 10-year window and climate synchrony values for every pair of sites for each 10-year window) and associated R code are available in the Mendeley Digital Repository (https://doi.org/10.17632/fswbjm7kth.1)

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108610https://doi.org/10.1016/j.ecolind.

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