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# Towards a measure of functional connectivity: Local synchrony matches small scale movements in a woodland edge butterfly

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# Abstract

This study investigates the sensitivity of local synchrony to movement patterns of the Ringlet butterfly (*Aphantopus hyperantus*). We examine whether population synchrony, describing the correlated fluctuations of conspecific populations, may prove an effective surrogate measure for monitoring functional connectivity in this species without the requirement of exhaustive sampling. We compared the effect on population synchrony of two different distance measures, direct (Euclidean) distance and distance via woodland rides and edges, and also of habitat matrix composition. Population synchrony of *A. hyperantus* was calculated as the pairwise correlation between population time-series using 20 years of data from UK butterfly monitoring scheme transects. Local population synchrony was better explained by distance via woodland edges than direct distance, especially for woodland-dominated transects. These results are consistent with mark-recapture data previously collected on the Ringlet butterfly. The results indicate a sensitivity of population synchrony to butterfly local dispersal behaviour, particularly, to the use of habitat corridors and other functional dispersal routes. Population synchrony is considered to have potential as a surrogate measure of functional connectivity. With development, this method could become a valuable conservation tool for identifying important landscape features which promote species' connectivity.

***Key-words:*** *Landscape permeability; Dispersal corridors; Habitat matrix; Population synchrony; Aphantopus hyperantus*

# Introduction

The importance of population connectivity for the persistence and conservation of metapopulations is widely recognised (Hanski and Gilpin, 1997; Roland et al., 2000; Moilanen and Hanski, 2001; Casula, 2006). The more well-connected the populations are, the greater the opportunity for dispersal, colonisation and re-colonisation of habitat patches, thereby reducing the risk of extinction (Hanski, 1994; Hanski, 1999; Chardon et al., 2003). Connectivity can be assessed as ‘structural’, considering landscape structure irrespective of species use or, as in this study, ‘functional’, inferring the movement of the study species through the landscape (Tischendorf and Fahrig, 2000).

Assessing functional connectivity is vital in monitoring and predicting the effects of changing climate and increasing habitat fragmentation on population persistence (Schtickzelle and Baguette, 2003; Sutcliffe et al., 2003), and in designing and managing conservation areas (e.g. identifying benefits of habitat corridors; Sutcliffe and Thomas; 1996; Haddad, 1999). Understanding and measuring dispersal constitutes an integral part of connectivity assessment both directly and in validating theoretical models. Currently, the collection of empirical dispersal data commonly involves mark-release-recapture (MRR) (Sutcliffe, Thomas and Peggie, 1997a; Roland et al., 2000; Sutcliffe et al., 2003; Casula, 2006; Oiun et al., 2008) or behavioural observations and radio-tracking of individuals (Sutcliffe and Thomas, 1996; Andreassen et al., 1998; Rubenstein and Hobson, 2004). These techniques can be invasive, labour-intensive, difficult to apply to multiple species and vary in success (e.g. a ‘poor’ year can result in insufficient data to infer movements, see Ricketts, 2001). More recent techniques include analysing genetic dissimilarity between populations to infer dispersal and connectivity, however, this again is labour-intensive and results can be confounded by temporal as well as spatial factors affecting genetic divergence (Schwartz et al., 2002; Clegg et al., 2003; Keyghobadi et al., 2005). The ability to rapidly and cost-effectively assess dispersal, and thus both connectivity and consequent population vulnerability to habitat change, through existing, readily-accessible datasets would therefore be highly beneficial to metapopulation conservation.

Population synchrony, measured as a correlation between different time-series of population abundances with no lag period (Bjørnstad et al., 1999), is a widely studied phenomenon in populations of animals and plants (Sutcliffe et al., 1996; Ranta et al., 1997; Swanson and Johnson, 1999; Paradis et al., 2000; Post and Forchhammer, 2004; Fontaine and Gonzalez, 2005; Kerlin et al., 2007; Kiviniemi and Löfgren, 2009). Synchrony is known to be caused by at least three processes: dispersal, correlated environmental stochasticity ("The Moran effect", e.g. climate) and trophic interactions (Hanski and Woiwod, 1993; Sutcliffe et al., 1997b; Bjørnstad et al., 1999; Hudson and Cattadori, 1999; Koenig, 1999; Liebhold et al., 2004; Raimondo et al., 2004) and can occur at scales ranging from local populations (within 1 $km^2$) to national or global scales. The exact contribution of dispersal to the spatial scale of synchrony, relative to the Moran effects, depends on the strength of density regulation (Lande et al., 1999; Kendall et al., 2000) and the mobility of the study organism (e.g. Paradis et al., 1999). It is generally acknowledged that dispersal will have greater effect at local scales (Sutcliffe et al., 1996; Benton et al., 2001). The effect of dispersal on populations may be positive or negative. Dispersal of even a few individuals can be sufficient to synchronise two populations governed by the same density-dependent processes (Liebhold et al., 2004), which can increase vulnerability to synchronised extinction by stochastic processes (Hanski and Woiwod, 1993; Benton et al., 2001). Conversely, exchange of individuals between populations ensures re-colonisation, gene-flow and reduces this vulnerability relative to a population synchronised through climate factors alone (Hudson and Cattadori, 1999). Generally however, the ability of dispersal to produce robust, persistent metapopulations will probably outweigh risks of synchronised global extinction.

Butterflies present an excellent candidate for this study as they are recognised as sensitive to changes in habitat (e.g. fragmentation) and climate (Gonzàlez-Megíaz et al., 2008; Haddad et al., 2008; van Swaay et al., 2008), and fluctuations in this group are indicative of responses in other taxa (Thomas, 2005). Many population connectivity studies have focussed on Lepidoptera (e.g. Moilanen and Hanski, 1998; Chardon et al., 2003; Schtickzelle and Baguette, 2003; Sutcliffe et al., 2003; Schneider and Fry, 2005; Casula, 2006; Ouin et al., 2008) as their movement patterns are highly influenced by local topological and habitat structural features (e.g. Kuefler and Haddad, 2006). Two primary determinants of population connectivity in butterflies are (i) distance- with increasing distance between sites tending to decrease connectivity (Sutcliffe et al., 1997a; Roland et al., 2000; Ouin et al., 2008); and (ii) the intervening habitat matrix- with higher quality habitat increasing permeability of the habitat to movement (Ricketts, 2001; Schtickzelle and Baguette, 2003; Sutcliffe et al., 2003; Roland and Matter, 2007; Powney et al., 2011). These two factors are not mutually exclusive, and omitting one, particularly habitat, may overestimate the influence of the other (Roland et al., 2000; Chardon et al., 2003). Small-scale movement patterns in the Ringlet (*Aphantopus hyperantus* L.) indicate sensitivity to habitat structure. In particular, Sutcliffe and Thomas (1996) found distance via woodland rides to be significantly better than Euclidean distance at explaining inter-patch movements in this species, highlighting the potential of habitat corridors in connecting populations. This importance of landscape structure on the small scale movements of individuals has also been found in populations of woodland birds in Britain (Bellamy et al., 2003).

Functional connectivity and population synchrony are strongly related, the latter caused, at least partly, by the former. As with connectivity, synchrony has been recognised to broadly decline with increasing distance between populations (Moran, 1953; Hanski and Woiwod, 1993; Raimondo et al., 2004; Kerlin et al., 2007; Kiviniemi and Löfgren, 2009). However, while the established trend with Euclidean distance has been widely discussed, fewer measures of ‘functional’ distance reflecting likely routes taken between populations by the study organism have been investigated. Roland and

Matter (2007) used synchrony in population dynamics to measure the impact of encroaching forest on the connectivity of alpine meadow butterfly populations at distances up to 8 km apart. They found that distance around forest, not Euclidian distance, best determines synchrony, suggesting that forest reduces butterfly movement. Powney et al. (2011) examined how population synchrony relates to landscape structure at larger spatial scales (distances of up to 200km apart). Populations separated by landscapes with smaller amounts of suitable habitat showed less synchronised dynamics, suggesting that at larger spatial scale population synchrony may be a useful tool for measuring functional connectivity.

Using long-term counts within nine southern England transects, this study aims to evaluate the possibility of using inter-annual population synchrony to measure local movements of *A. hyperantus* at a smaller spatial scale than Roland and Matter (2007) or Powney et al. (2011). Population synchrony is then related to functional distance and the results are discussed in relation to the results of a MRR study by Sutcliffe and Thomas (1996). We compare the effect of (i) direct (Euclidean) distance with (ii) distance via woodland rides and edges, on population synchrony. Habitat similarity has previously been indicated to promote synchrony (e.g. Sutcliffe et al., 1997b; Paradis et al., 1999). Therefore to account for any variation due to habitat, the habitat similarity of the occupied patches and the intervening habitat matrix will also be assessed. We aim to assess the suitability of using population synchrony to measure small scale movements of butterflies in an intensively managed landscape. We predict that population synchrony will be better explained by woodland edge distance rather than Euclidean distance. This is because woodland edge distance represents a more accurate measure of the actual movement patterns of Ringlet butterflies between habitat patches than Euclidean distance.

# Methods

## Study species

All synchrony analyses were conducted for *A. hyperantus*, a butterfly with a well-documented ecology and widespread distribution in the UK (Fox et al., 2006). *Aphantopus hyperantus* are univoltine and tend to inhabit woodland-edge, grassland and scrub habitats (Pollard, 1991). The species has local distributions that exhibit both metapopulation and 'patchy aggregation' attributes (Sutcliffe et al., 1997a). Previous research has shown *A. hyperantus* to be sensitive to minor variations in microhabitat (e.g. Sutcliffe et al., 2003).

## Synchrony analysis

### *Study Site Selection*

We analysed nine UK Butterfly Monitoring Scheme (UKBMS) transects in southern England that satisfied the following criteria aimed at ensuring data quality: a) population time-series of greater than seven years (Sutcliffe et al., 1996) where abundance counts were recorded in all three regional peak weeks (see next section), b) digital maps detailing transect section positions were available (http://www.ukbms.org/), and c) the transect was divided into more than three sections, with broad habitat classification data available for each section. Transect locations are illustrated in Figure 1.

#Figure 1 (a and b) approximately here #

### *Data collection and preparation*

Annual *A. hyperantus* abundance counts recorded between 1987 and 2007 were extracted from the UKBMS database and analysed for local synchrony between all possible pair-wise section combinations within each transect. All transects are divided to sections (see Fig. 2), usually consistent with different habitat or topology, and the number of adult butterflies observed are recorded for each section, each week, in appropriate weather conditions for 26 weeks between April and September (see Pollard and Yates, 1993 and van Swaay et al., 2008 for detailed methods). To standardise uneven sampling effort across transects (some weeks were missed by recorders on certain transects), the annual ‘peak’ three weeks, with the highest abundance counts at county level, were determined and, for each transect, only years with recorded data in all three regional peak weeks were analysed.

#Figure 2 approximately here#

In addition to the master dataset including all transect data, those transects composed predominantly (>70% of total transect length) of woodland (*n* = 4) and of grassland (*n* = 5) were separated to create two more datasets. The ‘woodland’ and ‘grassland’ datasets allowed us to explore if the relative effect of Euclidean and woodland-edge distance differed depending on transect type.

### *Synchrony calculation*

For each transect, a time-series of summed abundance counts over the three regionally determined peak weeks (e.g. each year contains data summed over three weeks) was produced for every section. To reduce the effects of yearly global synchronising factors (such as climate) on the time-series and therefore optimise the sensitivity of the synchrony analysis to local landscape metrics, the time-series data were ‘pre-whitened’, using the following equation adapted from Paradis et al., (1999; 2000):

$$d_{it} = c_{it} - m_i I_t \qquad [1]$$

where $d_{it}$ is the pre-whitened count in transect section *i* for year *t*, $c_{it}$ is the raw abundance count for section *i* at year *t*, $m_i$ is the mean abundance of section *i,* and $I_t$ is the global population index for year *t*. For the global population index we used the UKBMS national collated index, which is an index of annual abundance compiled from all transects across the England (Rothery and Roy 2001). This national time-series was standardised to fluctuate around 1 by subtracting the overall mean (*m*) from each data point (*n*) and then adding 1 as shown in the following equation:

$$I_t = (n_t - m) + 1 \qquad [2]$$

Hence, changes in the local population time-series in the same direction as the national population trend are given less weight, whereas changes in the opposite direction to the national trend are given more weight. For each section pair in every transect, a Spearman's rank correlation co-efficient was calculated on the pre-whitened abundance counts (as in Sutcliffe et al., 1996) as a measurement of local-scale synchrony. Statistical non-independence of these comparisons was dealt with using randomisation tests (see Statistical Analysis section).

### *Calculation of distance and habitat measures*

Two distance measures were calculated for each section pair, ‘Direct distance’, measured as the Euclidean distance between section midpoints; and ‘Woodland-edge distance’, calculated as the shortest distance between section midpoints via woodland rides or woodland edges. Where continuous woodland-edges/rides were not present between sections, either direct distances between woodland fragments or sections were used, except, in the presence of large natural boundaries such as wide rivers, lakes or tall hedgerows, when distance along these boundary edges was measured instead. All distances were calculated using ArcGIS (ArcMap™ version 9.2). Mean direct distances between section mid-points of transects used in this study were 508.30 m ± 14.35 [SE] (range: 32.28 – 1397.27 m), whilst woodland-edge distances between section mid-points were 698.99 m ± 20.69 [SE] (range: 36.44 – 2205.77 m).

To account for any variation attributable to spatial variation in habitat features, two variables were assessed: ‘Habitat Similarity’ and ‘Habitat Matrix’. The inclusion of habitat similarity accounts for similar habitat types on transects which may cause similar population dynamics and, therefore, increased population synchrony (Sutcliffe et al., 1996; Powney et al., 2010). The habitat type of each section was classified by butterfly recorders as one of eight habitat categories: arable, broadleaved woodland, bare ground/ exposed rock, fen/bog, heathland, hedgerow/ tall- herb/ mosaic habitats, improved grassland, unimproved grassland. These broad categories were aimed at describing the main habitat type that was present on each transect section. Habitat similarity was designated on whether the paired transect sections had the same (“Y”) or different (“N”) habitat classifications. The habitat matrix represents the major habitat type on a straight line between the midpoints of each section pair, classified using digital map data and can be one of three of the following categories: where the dominant habitat (> 80%) consisted of: (1) Grassland; (2) Woodland; or (3) Mixed habitat, if no single habitat type showed a >80% dominance.

### *Statistical Analysis*

The relative effects of the distance and habitat measures on local synchrony were assessed for three data sets: (i) all transects combined ($n = 9$), (ii) woodland-dominated transects ($n = 4$), and (iii) grassland-dominated transects ($n = 5$). A Pearson's correlation test of Direct Distance and Woodland-edge Distance found the variables to be highly correlated ($r = 0.927$; $p < 0.001$) and to avoid potential problems due to colinearity, these measures were assessed separately using the following linear mixed effects models with transect included as a random effect in both models:

$$\text{Local Synchrony} = \text{Habitat Similarity} + \text{Habitat Matrix} + \text{Direct Distance} \qquad [3]$$

$$\text{Local Synchrony} = \text{Habitat Similarity} + \text{Habitat Matrix} + \text{Woodland-edge Distance} \qquad [4]$$

The two distance models were compared using Akaike's information criterion (AIC, Burnham and Anderson, 2010). Since synchrony measures of pairwise transect sections are not independent, Mantel randomisation tests with $10^4$ permutations were conducted to determine the significance of individual predictor variables. At each permutation, response and predictor variables were randomised, a linear mixed effects model fitted, and the F-ratio extracted. A frequency distribution of the F-ratios was then plotted and the *p*-values for each variable calculated based on the position of the observed F-ratio in the distribution of these simulated values (e.g. a value in the top 5% of the F-ratio frequency distribution would have a significant *p*–value of <0.05). All statistical analyses were carried out using R.2.8.0 (R Development Core Team, 2008).

# Results

## The effect of direct or woodland-edge distance on population synchrony

Across all combined transects, population synchrony was found to significantly decrease with woodland distance whilst a negative, but non–significant, relationship was found with direct (Euclidean) distance (Euclidean distance-synchrony relationship: *F* = 2.38, *n* = 447, *Mantel p* = 0.125; woodland edge- synchrony relationship: *F* = 4.67, *n* = 447, *Mantel p* = 0.031; Figure 3; Table 1). The model with woodland-edge distance performed slightly better than direct distance in determining population synchrony (woodland edge- synchrony relationship AIC = 249.54; Euclidean distance-synchrony relationship AIC = 251.08; Table 2). When only woodland-dominated transects were assessed, woodland edge distance between sections was again found be significantly related to population synchrony (*F* = 4.02, *n* = 263, *p* = 0.044) while direct distance was insignificant (*F* = 0.90, *n* = 263, *p* = 0.349). In contrast, neither distance measure significantly explained variation in grassland-dominated transects synchrony (direct distance: *F* = 0.49, *n* = 184, *p* = 0.492; woodland-edge distance: *F* = 0.10, *n* = 184, *p* = 0.741; Table 1). For woodland-dominated transects, the woodland edge distance model performed better than the Euclidean distance model in determining population synchrony (woodland edge- synchrony relationship AIC = 167.68, Euclidean distance-synchrony relationship AIC = 170.01; Table 2). However, in grassland-dominated transects, the direct distance model out-performed the woodland edge distance model in determining population synchrony (woodland edge- synchrony relationship AIC = 112.14, Euclidean distance-synchrony relationship AIC = 111.15; Table 2), although neither measure of distance was statistically significant (Table 1). The mean level of synchrony was higher in grassland transects in comparison to woodland transects (mean synchrony = 0.309 and 0.267, respectively, Appendix 1).

#Table 1 approximately here#

#Table 2 approximately here#

#Figure 3 approximately here#

### The effect of habitat on population synchrony

Habitat similarity was not significantly correlated with synchrony in the statistical models analysing all transects together. However, in grassland-dominated transects, habitat similarity significantly affected synchrony in both distance models (direct distance $F = 9.26$, $n = 184$, $p = 0.002$, woodland edge distance $F = 9.17$, $n = 184$, $p = 0.002$). In woodland-dominated transects, habitat similarity was not correlated with synchrony in either distance model. Habitat matrix was significant in determining synchrony in both distance models across all transects combined and for woodland-dominated transects. However, habitat matrix was not significant in determining synchrony in either distance model for grassland-dominated transects (Table 1).

# Discussion

This study aimed to investigate the sensitivity of population synchrony to factors influencing local scale movements of butterflies. We found functional distance measures to be important in affecting local synchrony, with woodland-edge distance predicting synchrony patterns better in woodland-dominated landscapes than direct Euclidean distances. Habitat similarity between transects led to more synchronous population dynamics in grassland-dominated landscapes.

## Relationship between distance and local population synchrony

This study found that the distances along woodland-edges between transect sections predicted local synchrony better than direct Euclidean distances. Focusing on only the woodland transects, woodland-edge distance was found to be significant in explaining variation in synchrony between transect sections, whereas direct Euclidean distance was insignificant. Woodland-edge distances between transect section midpoints were on average about 160m longer than direct Euclidean distances. Hence, for woodland-edge distance to explain population synchrony better than direct distance suggests that butterflies use woodland-edge routes more frequently and that these journeys contribute to synchronising local population dynamics. This is consistent with results from MRR field studies of butterfly movement patterns (Sutcliffe and Thomas, 1996; Roland and Matter, 2007). Sutcliffe and Thomas (1996) showed that distance via woodland rides better explained *A. hyperantus* movement between woodland clearings than direct distance. Therefore, population synchrony appears to be sensitive to the local movement patterns of *A. hyperantus* in response to presence of suitable habitat features, such as corridors, which are recognised factors contributing to connectivity (Tischendorf and Fahrig, 2000; Ricketts, 2001; Schtickzelle and Baguette, 2003; Sutcliffe et al., 2003).

Local synchrony in grassland-dominated transects showed no significant trend with either distance measure. In addition, these transects on average showed higher mean levels of synchrony than woodland transects (Appendix 1). This lack of a distance-synchrony relationship, yet higher mean levels of synchrony, suggests that within the range of (relatively short) distances investigated in this study, populations in grassland-dominated transects are equally well-connected irrespective of distance.

The average (and maximum) distances travelled by *A. hyperantus* males (females travelled shorter distances) in the Sutcliffe et al. (1997b) MRR study were substantially lower than those inferred in our synchrony analysis, even though the results, identifying woodland as a barrier to dispersal, were qualitatively similar. Hence, our synchrony analysis method appears to provide robust results at larger spatial scales, over which time-intensive MMR studies would be infeasible.

Influences of habitat matrix on synchrony-distance relationships can be detected over even larger spatial scales. Roland & Matter (2007) found that encroaching forests can decouple butterfly population dynamics up to 4km apart. Powney et al. (2011) found that at larger spatial scales (up to 200 km apart), populations separated by more suitable landscape also showed more synchronised dynamics. The geographic scale of our study bridges the finer scale MMR work of Sutcliffe et al. (1997b) and larger scale synchrony analyses of Roland & Matter (2007) and Powney et al. (2011), providing strong evidence that population synchrony could potentially be a valuable measure of functional connectivity across a range of spatial scales.

## The effect of habitat on population synchrony

Synchrony was found to be significantly higher between sections with the same habitat type for grassland-dominated transects. This is congruent with previous research, for example, Sutcliffe et al. (1997b) showed at a local scale that *A. hyperantus* in certain habitats suffered synchronous local extinction following drought. Powney et al. (2010) also found that similar habitat types promoted synchrony between populations of the Speckled Wood butterfly *Pararge aegeria*. Populations of butterflies in similar habitat types may share characteristic dynamics, due to similar population growth parameters (i.e. birth rates, death rates; Liebhold et al. 2006), and also through similar responses to environmental perturbations. In contrast, different habitat types may support a more varied range of population dynamics. Such patterns have been suggested to explain the observation of more stable populations in heterogeneous landscapes; a range of different habitats leads to an averaging effect with lower overall population variability (den Boer, 1981; Thomas, 1991; Oliver et al., 2010). Linking the two concepts of population variability and synchrony, bird populations that are more variable over time tend to show increased synchrony (Paradis et al., 2000). Although this relationship has not yet been directly explored in butterflies, butterfly populations at geographic range margins are more variable (Thomas et al., 1994, Oliver et al., 2012) and also tend to show higher synchrony between populations (Powney et al., 2010). No significant relationship was found between habitat similarity and synchrony in woodland-dominated transects. It may be the case that in our broad habitat classifications there is more internal variation in the woodland classification than in grassland classification. For example, woodland habitats may have more heterogeneous management regimes (over time and space) than grassland habitats. This area of study would benefit from further work to understand the lack of relationship between synchrony and habitat similarity in woodland transects.

Many dispersal modelling studies have found intervening habitat matrix structure and quality to have a significant effect on butterfly dispersal (Roland et al., 2000; Ricketts, 2001; Chardon et al., 2003; Sutcliffe et al., 2003; Schneider and Fry, 2005; Powney et al 2011). In our model we found habitat matrix was an important predictor of synchrony in woodland-dominated transects and for all transects combined. Sections separated by mixed habitat showed lower levels of synchrony than those separated by a matrix primarily containing either woodland or grassland. This may be due to the impermeable nature of agricultural and urban land which often constituted the matrix in the mixed categories. Woodland regions in this study contain rides and paths which will increase permeability, while grassland habitat is unlikely to inhibit dispersal, which is emphasised by the increased mean level of synchrony in grassland-dominated transects.

### Synchrony as a measure of small-scale butterfly movements

The sensitivity of synchrony to the difference between direct and woodland-edge distance indicates promising potential for the use of synchrony to assess functional connectivity. This study has not only produced the same result using synchrony analysis as Sutcliffe and Thomas (1996) found using MRR data, but it has detected the effect of woodland rides operating at much larger scales than shown by previous research. This result adds support for the use of synchrony in larger scale analyses that would be more difficult and impractical using MRR.

## Limitations

There are several limitations to the present study methodology which if resolved, may improve synchrony performance as a connectivity monitoring measure.

### *Synchrony data availability*

Under the strict criteria and focus of this study, the number of usable transects was far fewer than the total number available, limiting the dataset size. With a broader focus, data availability need not be a limitation. Many recording schemes hold large spatial population time-series datasets which could be exploited for this kind of analysis.

### *Other causes of synchrony*

Environmental stochasticity and trophic interactions are also recognised to cause population synchrony (e.g. Bjørnstad et al., 1999) and separating dispersal from these effects is notoriously problematic (Kendall et al., 2000; Kiviniemi and Löfgren, 2009). National climate trends were addressed by conducting analyses on pre-whitened data and at a local scale, where movement of individuals has a greater effect than climate (Sutcliffe et al., 1996). However, local density-independent events such as local climate or coincident management of paired transect sections may still affect synchrony. Furthermore, trophic interactions are inextricably linked to dispersal and climate, as these processes simultaneously affect natural predators/prey, and hence may also be unavoidably affecting population synchrony. However, it is encouraging that the results from our local synchrony measure appear similar to results based on actual butterfly dispersal data from a MRR study.

## Further study

At present population synchrony exhibits potential as a connectivity measure. It would be interesting to incorporate analyses of more species, perhaps to contrast generalist and habitat specialists as a test of sensitivity to varying butterfly dispersal behaviours. Also, the direct comparison of synchrony with dispersal data, for example where MRR dispersal data and synchrony have been collected/calculated on the same paired transect sections, would prove an informative and thorough validation of this technique. Field surveys or higher resolution remote sensing data (e.g. LIDAR) may improve estimates of habitat types and boundary features that promote connectivity and is an ideal area for future work.

## Conservation implications

The ability to assess and monitor population connectivity using existing data, rather than labour-intensive and invasive MRR techniques, would be highly beneficial to conservation efforts, particularly with the increasing threat of climate change and habitat fragmentation on population persistence. Furthermore, with development, the ability to carry out synchrony studies at large geographic scales (Pollard and Yates, 1993; Hanski and Woiwod, 1993) would potentially facilitate landscape scale analyses of connectivity, a task for which MRR techniques are clearly unsuitable. One use of our technique could be to identify the salient landscape features that promote connectivity for a given species across a particular region (if sufficient population monitoring locations exist within the region to provide input data for the analysis). In addition, mean local synchrony could be calculated for many different species across the region and used as a surrogate measure of species mobility. This mobility trait would be a combination of species dispersal ability and the permeability of the monitored landscape to the focal species.

Although the present analysis of synchrony does not support the immediate adoption of this measure, improvements have been suggested and with development may produce an analytical tool with which functional connectivity and consequent population vulnerability to extinction may be assessed without requirement of exhaustive and invasive sampling techniques.

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# Tables

**Table 1** Significance of habitat and distance measures on Local Synchrony under different models of Habitat Similarity, Habitat Matrix and either Direct Distance or Woodland-edge distance. The significance of each predictor variable is indicated by the F-ratio and Mantel p-value.

| **Dataset**<br>**Predictor** | **Model 1 (Euclidean Distance)** | | | **Model 2 (Woodland-edge Distance)** | | |
|---|---|---|---|---|---|---|
| | **Coefficient** | **F** | **Mantel P** | **Coefficient** | **F** | **Mantel P** |
| *All transects* | | | | | | |
| Section habitat similarity | | 1.094 | 0.288 | | 1.114 | 0.303 |
| No | -0.009 | | | -0.008 | | |
| Yes | 0.008 | | | 0.007 | | |
| Habitat matrix | | 4.297 | **0.011** | | 4.297 | **0.019** |
| Grassland | 0.004 | | | 0.003 | | |
| Mixed | -0.045 | | | -0.047 | | |
| Woodland | 0.036 | | | 0.038 | | |
| Euclidean / Woodland Distance | -8.51x10$^{-5}$ | 2.383 | 0.125 | -8.36x10$^{-5}$ | 4.668 | **0.031** |
| *Grassland-dominated transects* | | | | | | |
| Habitat similarity | | 9.255 | **0.002** | | 9.168 | **0.002** |
| No | -0.044 | | | -0.046 | | |
| Yes | 0.055 | | | 0.057 | | |
| Habitat matrix | | 0.358 | 0.693 | | 0.363 | 0.694 |
| Grassland | -0.013 | | | -0.013 | | |
| Mixed | 0.017 | | | 0.015 | | |
| Woodland | 0.036 | | | 0.045 | | |
| Euclidean / Woodland Distance | -5.93x10$^{-5}$ | 0.493 | 0.492 | -1.99x10-$^{5}$ | 0.103 | 0.741 |
| *Woodland-dominated transects* | | | | | | |
| Habitat similarity | | 1.279 | 0.272 | | 1.277 | 0.244 |
| No | 0.023 | | | 0.023 | | |
| Yes | -0.014 | | | -0.014 | | |
| Habitat matrix | | 4.811 | **0.014** | | 4.861 | **0.010** |
| Grassland | 0.021 | | | 0.002 | | |
| Mixed | -0.082 | | | -0.085 | | |
| Woodland | 0.038 | | | 0.040 | | |
| Euclidean / Woodland Distance | -7.13x10$^{-5}$ | 0.890 | 0.349 | -1.03x10$^{-4}$ | 4.019 | **0.044** |

**Table 2** The Log Likelihood, sample size (n) and AIC from statistical models relating local synchrony to Habitat Similarity, Habitat Matrix and either Direct Distance or Woodland-edge distance

| Dataset | Distance measure | Log Likelihood | n | AIC |
|---|---|---|---|---|
| All transects | Woodland edge | -117.77 | 447 | 249.54 |
| | Euclidean | -118.54 | 447 | 251.08 |
| Grassland-dominated transects | Woodland edge | -49.07 | 184 | 112.14 |
| | Euclidean | -48.57 | 184 | 111.15 |
| Woodland-dominated transects | Woodland edge | -76.84 | 263 | 167.68 |
| | Euclidean | -78.01 | 263 | 170.01 |

**Fig.1** Distribution of **i)** analysed transects within the UK, and **ii)** individual transects within the UK counties (Oxfordshire, Buckinghamshire and Cambridgeshire): Aston Rowant North, ARn; Aston Rowant South, ARs; Aston Upthorpe Downs, AU; Burnham Breeches, BB; M40 Compensation Area, M40; Monks Wood, MW; Shabbington Wood, SW; Waterperry Wood, WW; and Wytham, W.

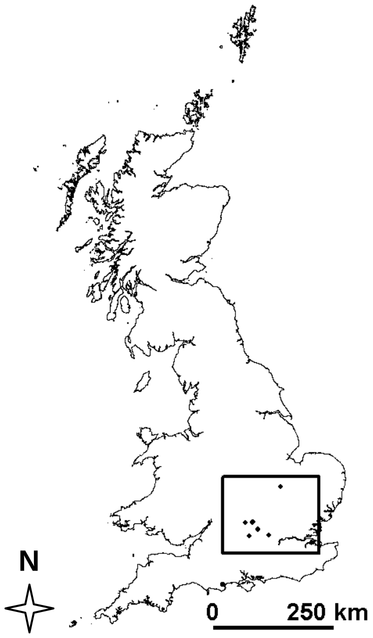
**Fig.2** Monks Wood transect sections (for all transect recording routes see www.ukbms.org).

**Fig.3** Relationship of residual synchrony (after accounting for Habitat Similarity and Habitat Matrix) with **i)** direct; and **ii)** woodland-edge distance for all transects combined. Points represent the mean residual synchrony for each 100m block for Euclidean distance and each 200m block for Woodland edge distance with standard error bars.

# Figures

Figure 1

i)



ii)

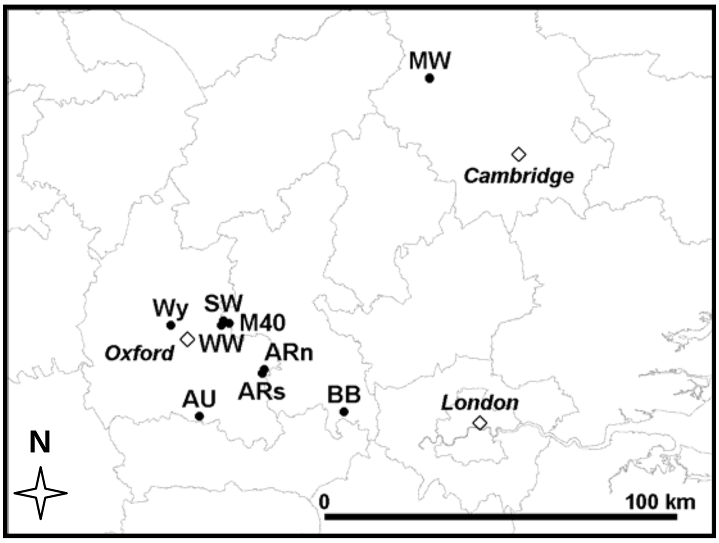


Figure 2

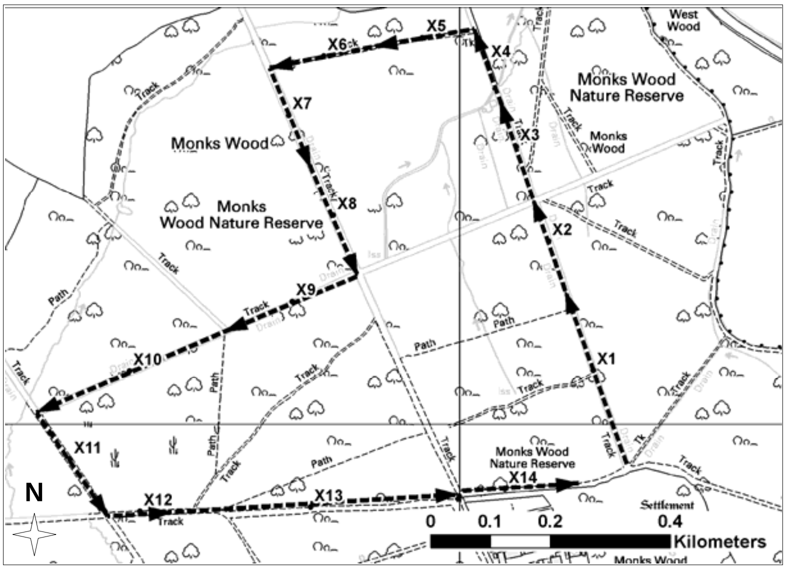
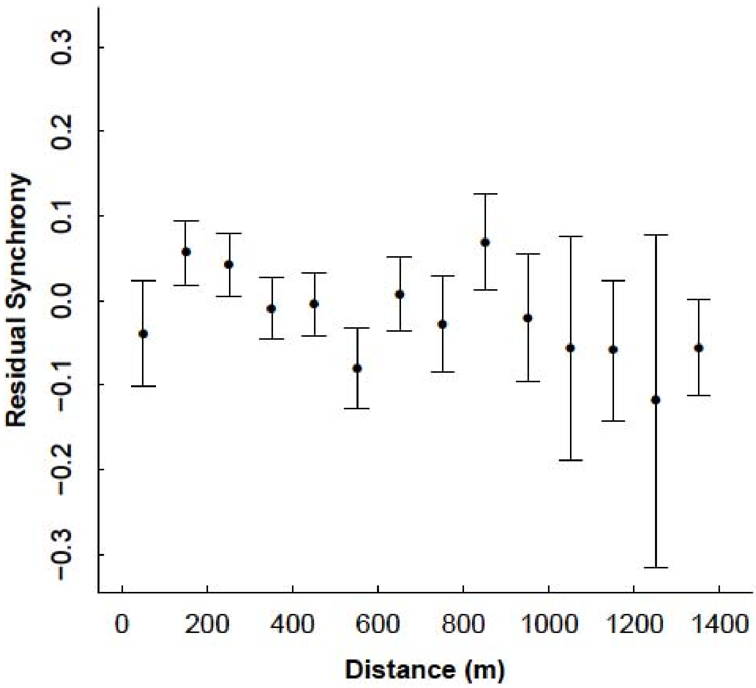
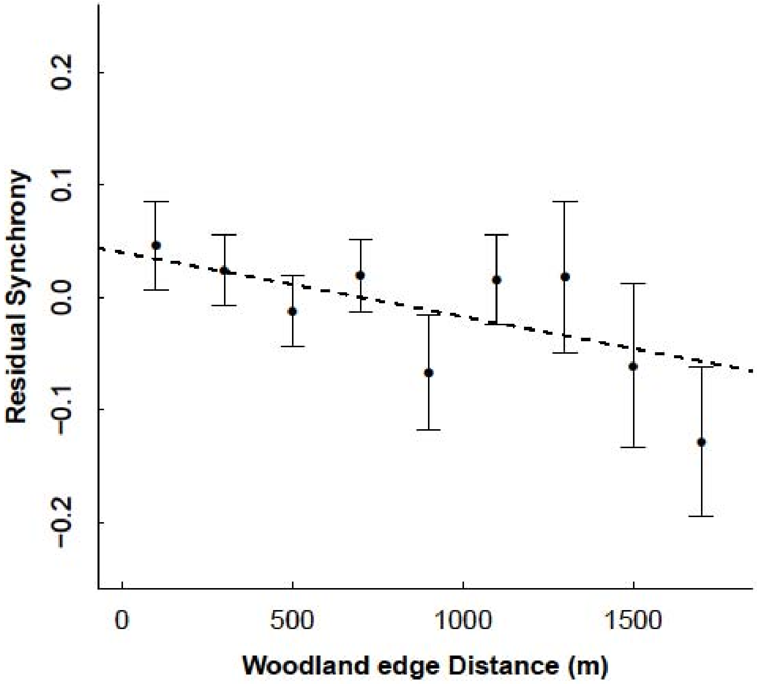

West Wood
X5
X6
X4
Monks Wood Nature Reserve
X7
X3
Monks Wood
Monks Wood
X8
Monks Wood Nature Reserve
X2
X9
X1
X10
X11
Monks Wood Nature Reserve
X14
N
X12
X13
Settlement
Track
Path
Drain
0
0.1
0.2
0.4
Kilometers
Monks Wood

Figure 3

i)


Residual Synchrony
−0.3
−0.2
−0.1
0.0
0.1
0.2
0.3
0
200
400
600
800
1000
1200
1400
Distance (m)

ii)


Residual Synchrony
−0.2
−0.1
0.0
0.1
0.2
0
500
1000
1500
Woodland edge Distance (m)

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## Appendices

Appendix 1. The mean values of synchrony and the two distance measures for each of the three dataset collections.

| | **Mean synchrony** | **Mean Euclidean distance** | **Mean woodland edge distance** |
|---|---|---|---|
| All transects | 0.285 | 508.3 | 699.0 |
| Grassland transects | 0.309 | 492.5 | 628.4 |
| Woodland transects | 0.267 | 519.4 | 748.4 |