

## Article (refereed) - postprint

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Oliver, Tom H.; Powney, Gary D.; Baguette, Michel; Schtickzelle, Nicolas.  
2017. **Synchrony in population counts predicts butterfly movement  
frequencies.** *Ecological Entomology*, 42 (3). 375-378. [10.1111/een.12391](https://doi.org/10.1111/een.12391)

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[noraceh@ceh.ac.uk](mailto:noraceh@ceh.ac.uk)

# Synchrony in population counts predicts butterfly movement frequencies

**Tom H. Oliver<sup>1,2\*</sup>, Gary D. Powney<sup>2</sup>, Michel Baguette<sup>3</sup>, Nicolas Schtickzelle<sup>4</sup>**

<sup>1</sup> *University of Reading, Whiteknights, PO Box 217, Reading, Berkshire, RG6 6AH, United Kingdom*

<sup>2</sup> *NERC Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK*

<sup>3</sup> *Muséum National d'Histoire Naturelle, UMR 7205 Institut de Systématique, Evolution et Biodiversité, France.*

<sup>4</sup> *Earth and Life Institute, Biodiversity Research Centre, Université catholique de Louvain, Louvain-la-Neuve, Belgium*

\* Corresponding author email: [t.oliver@reading.ac.uk](mailto:t.oliver@reading.ac.uk)

## **Abstract**

Measuring functional connectivity, the ability of species to move between resource patches, is essential for conservation in fragmented landscapes. However, current methods are highly time consuming and expensive. Population synchrony- the correlation in time series of counts between two long-term population monitoring sites, has been suggested as a possible proxy measure of functional connectivity. To date, population synchrony has been shown to correlate with proxies for movement frequency such as the coverage of suitable habitat types in intervening landscapes, and also least cost distances around hostile land cover types. This provides tentative evidence that synchrony is directly driven by movements of the focal species, but an alternative explanation is that these land cover types affect the movement of interacting species (e.g. natural enemies of the focal species) which can also drive synchronous population dynamics. Therefore, what is needed is a test directly relating population synchrony to movement frequencies of a focal species. Here we use data from a 21 year mark-release-recapture study and show that population synchrony does indeed predict movements of a focal butterfly species *Boloria eunomia* (Esper). There is growing evidence that population synchrony can be a useful conservation tool to measure functional connectivity.

**Keywords:** functional connectivity, habitat fragmentation, landscape permeability, *Boloria eunomia*, long term monitoring data, mark release recapture

## **Introduction**

Understanding how the movement of organisms is affected by landscape change is central to the preservation and restoration of threatened populations in fragmented ecosystems.

Maintaining functional connectivity, the ability of a focal species to move between resource patches, is generally regarded as an essential goal of environmental conservation (Bennett, 1999; Crooks & Sanjayan, 2006). For example, functional connectivity is needed for recolonization of habitat patches and meta-population persistence (Hanski, 1999), and also allows species to shift ranges in response to climate change (Warren et al., 2001; Mair et al., 2014). Similarly some ecosystem services delivered by biodiversity (e.g. pollination and pest control) require an understanding of how species move across different landscapes.

Despite the clear importance of functional connectivity for managing species, ecosystem services and landscapes, current assessment methods are very limited. These include mark-release-recapture studies, which are time consuming and expensive and thus limited in their maximum spatial extent, and landscape genetics, which provides promise but is also currently expensive and has issues in that genetic divergence is determined by temporal as well as spatial separation (Storfer et al., 2010).

Population synchrony, the correlations in time series of counts between long-term population monitoring sites, has been advanced as an alternative method which can exploit spatially widespread, long-term monitoring data of the kind available from volunteer recording schemes (e.g. the UK Butterfly Monitoring Scheme [www.ukbms.org](http://www.ukbms.org); Powney et al., 2011; Powney et al., 2012). Population synchrony is driven by spatial autocorrelation in climate variables and biotic interactions that affect the focal species, and also by movement of the focal species between populations (Moran, 1953; Hanski & Woiwod, 1993; Sutcliffe et al., 1996; Bjørnstad et al., 1999; Cattadori et al., 2005; Vogwill et al., 2009). Hence, using population synchrony as a proxy for species movements requires accounting for other factors.

Paradis et al (2000) and Powney et al (2011) used a method called ‘pre-whitening’ to reduce the effects of shared climate on synchrony across all populations. In contrast, the effects of biotic interactions are harder to account for, as putative landscape factors that may affect focal species movement may also affect movement of interacting species (e.g. natural enemies or mutualists).

To date, demonstrations of the potential of population synchrony to measure movement of focal species have shown correlations between population synchrony and the coverage of key habitat types in intervening landscapes (Powney et al., 2011) and least cost distances around hostile land cover types (Roland & Matter, 2007; Powney et al., 2012). These are promising but do not exclude the hypothesis that synchrony may be a proxy for the movement of interacting species rather than the focal species. Additional supporting evidence that synchrony may be a useful proxy for movement of focal species comes from studies showing higher average population synchrony scores for species that are more dispersive, measured by direct mark-recapture data (Paradis et al., 1999), or using dispersal-related morphological traits as proxies (e.g. wing span and body size for birds, Tittler et al., 2009; body size and hydrodynamic profile traits for fish, Chevalier et al., 2014). However, the best test for a single focal species would be to compare observed movements of individuals between patches with the synchrony in total abundance counts between patches.

Here, we do this for a 21 year butterfly mark-release-recapture (MRR) study from Prés de La Lienne, Belgium. Our hypothesis is that patches showing higher population synchrony will have a greater movement frequency of butterflies between them.

## Methods

We used data from a long-term study site at Prés de La Lienne, Belgium, where *Boloria eunomia* (Esper) butterflies were marked, released and recaptured from eight discrete habitat

patches each summer for 21 years. For full details of the sampling methodology see Schtickzelle & Baguette (2004). To assess butterfly movement frequency between patches, we created a matrix of between-patch movements summed from all capture-recapture data between 1992 and 2012. This provides an average estimate of inter-patch movement, smoothing out yearly variations due to factors such as weather (Schtickzelle et al., 2012).

To calculate population synchrony between patches, for each habitat patch, we calculated the total number of captures and recaptures per year. Within a habitat patch, we only counted individuals once even if they were captured several times in the same patch the same day, but individuals could be included in the daily count of several different habitat patches. With these data, we tested five metrics of population synchrony, involving increasing levels of ‘data cleaning’ to improve sensitivity to any signal from species movements. Initially, we simply considered the Pearson’s correlation in total yearly counts between 1992 and 2012, which were first standardised to unity (referred to hereafter as ‘standardised counts’). This metric was calculated for each pairwise combination of habitat patches ( $n = 36$ ). Next, we used two approaches for detrending the time series from each habitat patch. In the first approach we fitted a linear regression of count against year and used the residuals of this model to calculate the Pearson’s correlation coefficients between patches (Paradis et al., 2000; Powney et al., 2011; referred to hereafter as ‘detrended standardised count’). For the second approach we converted the population counts to growth rates using the following equation  $\log N_t - \log N_{t-1}$ , where  $N_t$  is the count in year  $t$  (Powney et al., 2010). We added 1 to all counts to avoid the problem of logging a zero count (referred to hereafter as ‘growth rates’). These detrending steps remove long term trends in population counts. Finally, after the detrending step, we additionally investigated the effect of ‘pre-whitening’ the data. This process takes differences between local patch time series and a ‘global index’ (here, the total annual population counts across the whole Prés de La Lienne system), in order to increase

sensitivity to differences in dynamics between local time series. We used the formula in Powney et al (2011; adapted from Paradis et al., 2000; see Appendix 1), and tested a range values for the scaling factor which modifies the extent to which local counts reflect the global index (Table S1). This pre-whitening step was tested for both the detrended- and the growth rate- time series (respectively, referred to hereafter as ‘pre-whitened detrended standardised counts’ and ‘pre-whitened growth rates’).

We then related these five measures of population synchrony to the observed butterfly movement frequency between patches using Mantel regressions, which account for non-independence of data from individual sites. We fitted observed frequency of inter-patch movements as the explanatory variable and population synchrony as the response. We used  $R^2$  scores as a measure of model goodness of fit, to assess the relative predictive ability of the different models and various scaling parameters, which gives the same result irrespective of axes order.

## **Results and Discussion**

We found a positive correlation between the frequency of movement of butterflies between habitat patches in the Prés de La Lienne system and the degree of synchrony in the long-term population time series (Table 1; Fig. 1). This provides good evidence that local population synchrony does reflect butterfly movements, rather than being solely driven by shared climatic influences or the functional connectivity of interacting species.

All three methods used to assess population synchrony gave qualitatively similar results, but the best method was through detrending population time series with a prewhitening step (Table 1; Fig 1). Calculating population synchrony on count data that were standardised to unity, we obtained an  $R^2$  value for the relationship between population synchrony and butterfly movement frequency of 0.09, using the de-trending method without pre-whitening

the  $R^2$  increased to 0.13, and with an additional pre-whitening step this increased substantially further to 0.29 (Fig 1; Table 1). This goodness of fit is stronger than found in previous butterfly studies relating synchrony to other proxies for movement (landscape suitability: Powney et al. 2011, least cost distances: Powney et al. 2012), perhaps because those latter variables are themselves only proxies of movement frequency. Although the goodness of fit of relationship does not lend itself to high confidence in the rates of movement between any two population monitoring sites based on the specific synchrony score, if data from multiple monitoring sites are available then population synchrony may still be very useful measure in identifying salient landscape characteristics that promote or hinder functional connectivity between sites. This could be achieved through the analysis of synchrony between each pairwise combination of population monitoring points and then relating these synchrony scores to landscape characteristics (i.e. area and configuration of different land cover types, through Mantel tests or associated approaches; e.g. see Storfer et al., 2010). Attention of course would need to be paid to whether landscape structure, and species' functional connectivity itself changes over the time period of study.

Evidence is accumulating that synchrony may be a feasible way to measure functional connectivity, at both small (e.g. below 10km; Roland & Matter, 2007; Powney et al., 2012) and large spatial scales (Powney et al., 2011). Therefore, long-term population monitoring data provide essential information not only on the status of species (Gregory et al., 2005; Brereton et al., 2011), but also on functional connectivity between monitoring sites. Notwithstanding this, detailed MRR studies such may still be necessary for high temporal resolution estimates of dispersal (Schtickzelle et al., 2012) and to calibrate (e.g. identifying the best pre-whitening scaling factor) and validate proxy measures.

## **Acknowledgements**



We thank the many field workers who assisted in sampling *B. eunomia* populations over the 21 year duration of this study. N.S. is research associate from the Belgian Fonds de la Recherche Scientifique-FNRS and acknowledges its financial support.

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## Tables

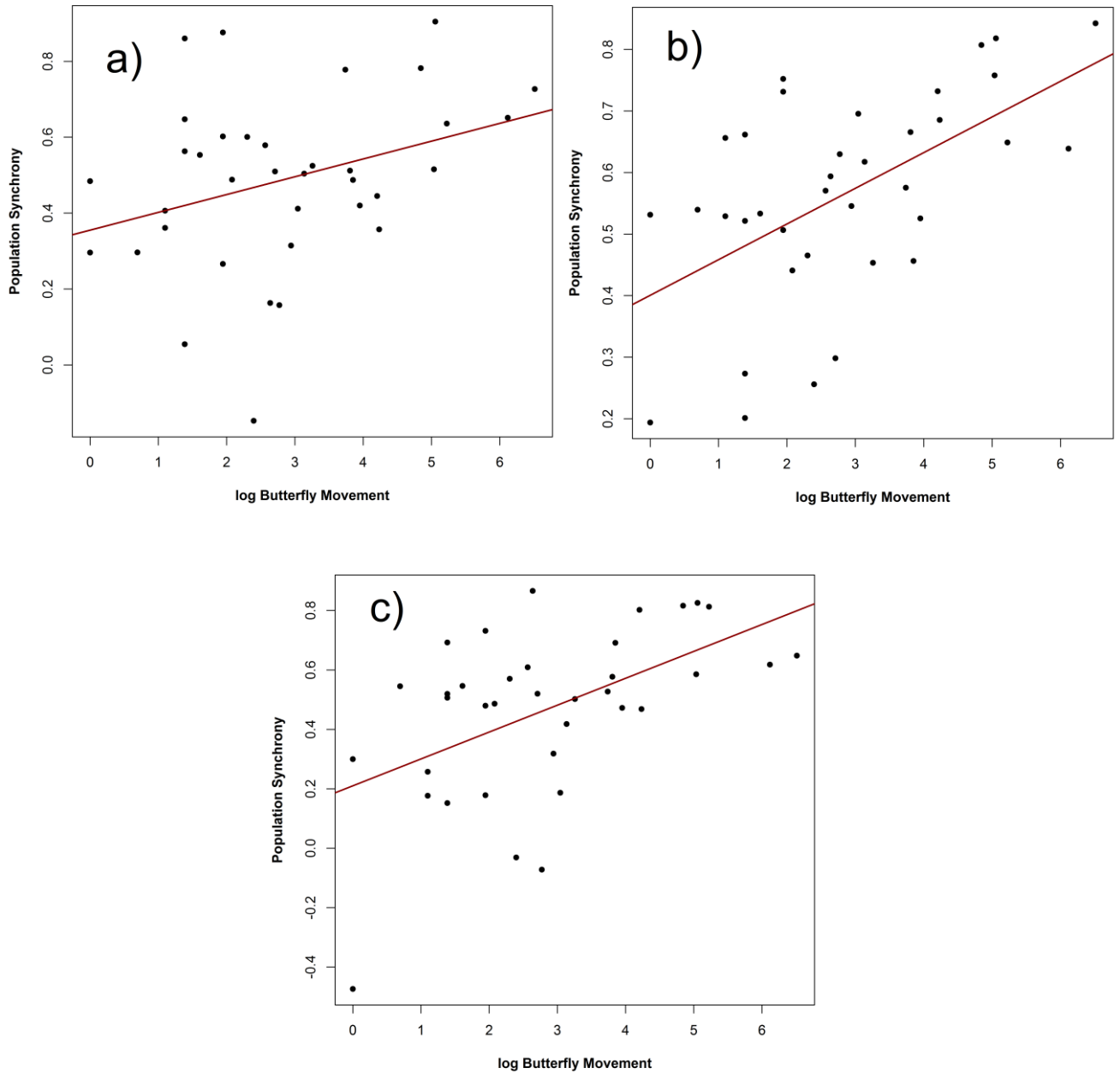
**Table 1**, Relationship between population synchrony and frequency of *B. eunomia* butterfly movement between patches in the Prés de La Lienne system, using alternative metrics to calculate population synchrony. For each metric, the scaling factor used here was identified as that which gave the highest goodness of fit from a sensitivity analysis (See Table S1 for full results).

Synchrony measured upon:	Scaling factor	Slope coefficient	s.e.	F	Mantel P	df	R <sup>2</sup>
Standardised count	none	0.047	0.023	4.25	0.047	34	0.09
Detrended standardised count	none	0.085	0.034	6.11	0.003	34	0.13
Pre-whitened detrended standardised count	3.5	0.058	0.015	15.46	<0.001	34	0.29
Growth rates	none	0.091	0.026	12.44	<0.001	34	0.25
Pre-whitened growth rate	0.5	0.089	0.025	12.11	<0.001	34	0.24

### Figure Legends

**Fig. 1,** The relationship between frequency of *B. eunomia* inter-patch movements and a) population synchrony calculated using detrended population counts standardised to unity, b) the previous metric with an additional step of ‘pre-whitening’ (see methods for explanations), and c) population synchrony calculated as growth rates. The  $R^2$  scores are 0.13, 0.29 and 0.25 respectively.

## Figures



**Fig. 1,** The relationship between frequency of *B. eunomia* inter-patch movements and a) population synchrony calculated using detrended population counts standardised to unity, b)

the previous metric with an additional step of ‘pre-whitening’ (see methods for explanations), and c) population synchrony calculated as growth rates. The  $R^2$  scores are 0.13, 0.29 and 0.25 respectively.