

SHORT COMMUNICATION

Synchrony in population counts predicts butterfly movement frequencies

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Abstract. 1. 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.

2. 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.

3. 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.

4. 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).

5. There is growing evidence that population synchrony can be a useful conservation tool to measure functional connectivity.

Key words. *Boloria eunomia*, functional connectivity, habitat fragmentation, landscape permeability, 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 recolonisation of habitat patches and metapopulation 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

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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; Powney *et al.*, 2011, 2012). Population synchrony is driven by spatial autocorrelation in climate variables and biotic interactions that affect the focal species, and also by the 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 a 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 the movement of interacting species (e.g. natural enemies or mutualists).

To date, demonstrations of the potential of population synchrony to measure the 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 the 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, a 21-year butterfly mark-release-recapture (MRR) study from Prés de la Lienne, Belgium is used. The present hypothesis is that patches showing higher population synchrony will have a greater movement frequency of butterflies between them.

Methods

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 were used. For full details of the sampling methodology see Schtickzelle and 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 (by subtracting the mean and dividing by the absolute maximum value; 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 counts’). 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.*, 2011). 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 steps, 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), 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 S1], and tested a range of values for the scaling factor which modifies the extent to which local counts reflect the global index (Table S1 in Appendix S1). This pre-whitening step was tested for both the detrended count- and the growth rate-time series (respectively, referred to hereafter as ‘pre-whitened detrended 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 the 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

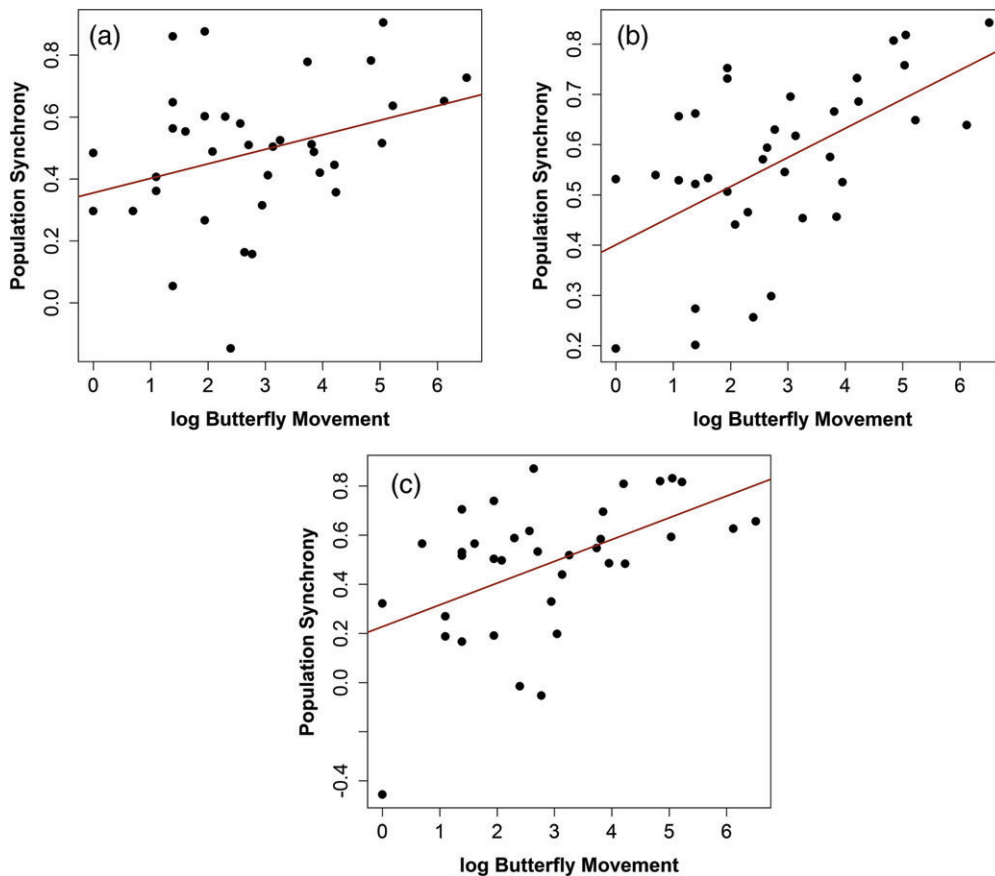
We found a positive correlation between the frequency of movement of butterflies between habitat patches in the Prés de la Lienne system and the degree of synchrony in the long-term population time series (Table 1; Fig. 1). This provides good evidence that local population synchrony does reflect butterfly 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

Table 1. Relationship between population synchrony and frequency of *Boloria eunomia* butterfly movement between patches in the Prés de la Lienne system, using alternative metrics to calculate population synchrony.

Synchrony measured upon:	Scaling factor	Slope coefficient	SE	<i>F</i>	Mantel <i>P</i>	d.f.	<i>R</i> ²
Standardised counts	None	0.047	0.023	4.25	0.047	34	0.09
Detrended counts	None	0.085	0.034	6.11	0.003	34	0.13
Pre-whitened detrended counts	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 rates	0.5	0.089	0.025	12.11	<0.001	34	0.24

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 in Appendix S1 for full results).

**Fig. 1.** The relationship between the frequency of *Boloria eunomia* inter-patch movements and (a) population synchrony calculated using detrended counts, (b) the previous metric with an additional step of ‘pre-whitening’ (see methods for explanations), and (c) population synchrony calculated using growth rates. The *R*² scores are 0.13, 0.29, and 0.25 respectively. [Colour figure can be viewed at wileyonlinelibrary.com].

a detrending population time series with a pre-whitening 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 detrending 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 demonstrated here still 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 a 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 change over the period of the study.

Evidence is accumulating that synchrony may be a feasible way to measure functional connectivity, at both small (e.g. below 10 km; 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 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.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12391

Appendix S1. Details of pre-whitening procedure and Table S1.

References

Bennett, A.F. (1999) *Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation*. IUCN, Gland, Switzerland and Cambridge, U.K.

Bjørnstad, O.N., Ims, R.I. & Lambin, X. (1999) Spatial population dynamics: analysing patterns and processes of population synchrony. *Trends in Ecology and Evolution*, **14**, 427–432.

Brereton, T., Roy, D., Middlebrook, I., Botham, M. & Warren, M. (2011) The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation*, **15**, 139–151.

Cattadori, I.M., Haydon, D.T. & Hudson, P.J. (2005) Parasites and climate synchronize red grouse populations. *Nature*, **433**, 737–741.

Chevalier, M., Laffaille, P. & Grenouillet, G. (2014) Spatial synchrony in stream fish populations: influence of species traits. *Ecography*, **37**, 960–968.

Crooks, K.R. & Sanjayan, M. (2006) *Connectivity Conservation*. Cambridge University Press, Cambridge, U.K.

Gregory, R.D., Van Strien, A., Vorisek, P., Meyling, A.W.G. & Noble, D.G. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, **360**, 269–288.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford, U.K.

Hanski, I. & Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology*, **62**, 656–668.

Mair, L., Hill, J.K., Fox, R., Botham, M., Brereton, T. & Thomas, C.D. (2014) Abundance changes and habitat availability drive species' responses to climate change. *Nature Climate Change*, **4**, 127–131.

Moran, P.A.P. (1953) The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Australian Journal of Zoology*, **1**, 291–298.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (1999) Dispersal and spatial scale affect synchrony in spatial population dynamics. *Ecology Letters*, **2**, 114–120.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. (2000) Spatial synchrony in populations of birds: effects of habitat, population trend, and spatial scale. *Ecology*, **81**, 2112–2125.

Powney, G.D., Chapman, D., Roy, D.B. & Oliver, T.H. (2011) Measuring functional connectivity using long term monitoring data. *Methods in Ecology and Evolution*, **2**, 527–533.

Powney, G.D., Broaders, L.K. & Oliver, T.H. (2012) Towards a measure of functional connectivity: local synchrony matches small scale movements in a woodland edge butterfly landscape. *Ecology*, **27**, 1109–1120.

Roland, J. & Matter, S.F. (2007) Encroaching forests decouple alpine butterfly population dynamics. *Proceedings of the National Academy of Sciences*, **104**, 13702–13704.

Schtickzelle, N. & Baguette, M. (2004) Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS. *Oikos*, **104**, 277–290.

Schtickzelle, N., Turlure, C. & Baguette, M. (2012) Temporal variation in dispersal kernels in a metapopulation of the bog fritillary butterfly (*Boloria eunomia*). *Dispersal Ecology and Evolution* (ed. by J. Clobert, M. Baguette, T. G. Benton and J. M. Bullock), pp. 231–239. Oxford University Press, Oxford, U.K.

Storfer, A., Murphy, M.A., Spear, S.F., Holderegger, R. & Waits, L.P. (2010) Landscape genetics: where are we now? *Molecular Ecology*, **19**, 3496–3514.

Sutcliffe, O., Thomas, C.D. & Moss, D. (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology*, **65**, 85–95.

Tittler, R., Villard, M.-A. & Fahrig, L. (2009) How far do songbirds disperse? *Ecography*, **32**, 1051–1061.

Vogwill, T., Fenton, A. & Brockhurst, M.A. (2009) Dispersal and natural enemies interact to drive spatial synchrony and decrease stability in patchy populations. *Ecology Letters*, **12**, 1194–1200.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B. *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

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