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Spatial synchrony is related to environmental change in Finnish moth communities

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Spatially distinct pairs of sites may have similarly fluctuating population dynamics across large geographical distances, a phenomenon called spatial synchrony. However, species rarely exist in isolation, but rather as members of interactive communities, linked with other communities through dispersal (i.e. a metacommunity). Using data on Finnish moth communities sampled across 65 sites for 20 years, we examine the complex synchronous/anti-synchronous relationships among sites using the geography of synchrony framework. We relate site-level synchrony to mean and temporal variation in climatic data, finding that colder and drier sites—and those with the most drastic temperature increases—are important for spatial synchrony. This suggests that faster-warming sites contribute most strongly to site-level estimates of synchrony, highlighting the role of a changing climate to spatial synchrony. Considering the spatial variability in climate change rates is therefore important to understand metacommunity dynamics and identify habitats which contribute most strongly to spatial synchrony.

1. Introduction

Populations fluctuate through time [1], and a central goal of population ecology has been to understand, quantify and relate these fluctuations to fundamental ecological processes such as predation [2], extinction risk [3] and environmental forcing [4]. Scaling processes acting on single populations, the study of spatial synchrony attempts to quantify how population time series are related [5–7]. There are three main putative drivers of spatial population synchrony. First, spatially autocorrelated environmental conditions can result in synchronous populations even when populations are thousands of kilometres away [8]. This phenomenon—often referred to as the Moran effect [9]—is well supported by both empirical [10–14] and theoretical [15,16] research. Second, dispersal between populations may synchronize paired populations [17–19]. Lastly, a mobile shared enemy capable of attacking paired populations may create synchronous population dynamics [20–23], as can interactions with other synchronous species. For instance, a parasite species with pronounced seasonal variation may influence local host population dynamics [24,25], as well as the synchrony between host populations [26]. These mechanisms, whether in isolation or combined, drive the resulting spatial synchrony. Disentangling the relative importance of these three mechanisms is an important question in ecology, as synchronous populations may be more likely to go extinct at the same time [5,27], suggesting an association between synchrony and (meta)population stability [5,9].

Identifying which local populations are *most* synchronous—or contribute most to spatial synchrony—may provide insight into the relative importance of habitat patches to the resulting spatial population dynamics. For instance, conservation or management actions designed to reduce or enhance synchrony, respectively, may benefit from targeting specific local populations. One way to assess the importance of individual populations to spatial synchrony across the entire spatial network is by combining the geography of synchrony approach [7] with measures from graph theory. Similar approaches have also been developed to examine variation in site-level contributions to spatial synchrony [28,29]. The geography of synchrony approach—specifically with respect to the incorporation of graph theory—builds a spatial network of local populations, which are connected to other populations based on their degree of synchrony (anti-synchrony), which can be measured given time series or across a rolling window. This spatial network can then be analysed using graph theoretic measures such as centrality, which quantifies the importance of each local population to the topological structure of the entire spatial network (i.e. metapopulation) [30]. This method has been used previously to examine the importance of particular areas in human cortical networks [31], site-level contributions to synchrony of bovine tuberculosis incidence [32] and large-scale spatial variation in vegetation [33] and marine phytoplankton [34] synchrony.

Estimating site-level contributions to spatial synchrony allows an examination of the associated spatial and environmental variables. More traditional approaches to the analysis of spatial synchrony use matrix regressions [5,35] or are based on pairwise data, which are incredibly useful and powerful, but do not provide a single measure for each site [36]. However, site-level measures incorporate information on all of the synchronous (anti-synchronous) interactions with other sites, creating a single measure which can be related directly to environmental or spatial gradients. Further, in addition to relating mean environmental conditions to synchrony estimates, the rate of change in environmental conditions may be important to temporal variation in the strength of spatial synchrony. For example, mean environmental conditions could be unrelated to site-level contributions to spatial synchrony, while the rate of environmental change may show a clear signal. This would suggest that sites contributing strongly (or weakly) to spatial synchrony are undergoing different rates of environmental change relative to other sites. Importantly, this could create a situation where the most important sites to driving spatial synchrony are also undergoing the most rapid environmental changes, with the potential to either reduce or enhance spatial synchrony in the future. While climate-induced synchrony is a fairly well-studied phenomenon [10,11,15,16], studies incorporating spatial differences in the rate of environmental changes and the resulting potential impacts are not yet developed.

In addition, species rarely exist in isolation, but more often as part of a larger community of interacting species. Combining data on multiple species may provide insight into interspecific differences in synchrony, which could then be related to dispersal ability, competition or sensitivity to environmental pressures. Studies focused on the drivers of spatial synchrony of a single important species are still quite valuable, but community-level data offer a number of intriguing research possibilities. First, synchrony can be calculated using the fluctuations in density of the entire

community. Competition and ecological drift may create fluctuations in single species dynamics which become undetectable when considering community density. Second, synchrony can be calculated for each species, and the importance of spatial locations to synchrony could be compared among species. That is, interspecific differences in species environmental tolerances (i.e. niches), spatial distribution, or life history traits may result in differences in the relative importance of each site to spatial synchrony. Lastly, synchrony networks could be formed for each species (as above), and then combined together to form one ensemble synchrony network. Links between sites then become the mean synchrony for all species shared between those two sites (i.e. communities), potentially removing some of the influence of demographic stochasticity on estimates of synchrony.

Here, we use data on Finnish moth communities surveyed across 65 sites for 20 years (1993–2012) to examine the spatial variability in local site relative importance to spatial synchrony networks. The spatio-temporal structure of the data allow estimation of the spatial variation in sites driving spatial synchrony. Using these extensive data, we create a single synchrony network, taking the mean synchrony value for all shared species between any two sites as a measure of synchrony. Using measures from graph theory, we demonstrate spatial variability in the relative importance of sampling sites to driving spatial synchrony. Further, we examine how mean and temporal variation in temperature and precipitation relate to site-level importance to spatial synchrony. We found that sites more important for spatial synchrony tended to be colder and drier. These sites corresponded to more northern locations, where temporal patterns in temperature change are also stronger. This suggests that currently cold sites—which are warming more quickly—are also those sites which contribute strongly to synchrony networks. Together, our findings provide a demonstration of the utility of the geography of synchrony approach to community data, highlight the clear existence of spatial variation in the temporal environmental change and site-level contributions to spatial synchrony, and identify a clear relationship between the importance that a site plays in maintaining spatial synchrony and both the mean and temporal variation in climatic conditions.

2. Methods

(a) Moth communities of Finland

Data on moth species abundances were gathered as part of the Finnish national moth monitoring scheme (Nocturna; an overview provided in [37]). Moth communities were sampled using light traps ('Jalas' model)—using either 160 W mixed light or 125 W mercury (Hg) vapour bulbs [38,39]—located mainly in forested areas, and run every night from early spring to late autumn (i.e. between April and October). Every week (or occasionally every other week), light traps were emptied and moth specimens were counted and identified to species by voluntary observers. Quality control of the data and cross-checking of moth identifications was carried out by the coordinating team at the Finnish Environment Institute (SYKE). A total of 208 trap sites were included in the monitoring network between 1993 and 2012. We examined a subset of 65 traps sampled in at least 8 years during the study period, so as to minimize temporal gaps in the community time series, as these gaps could influence

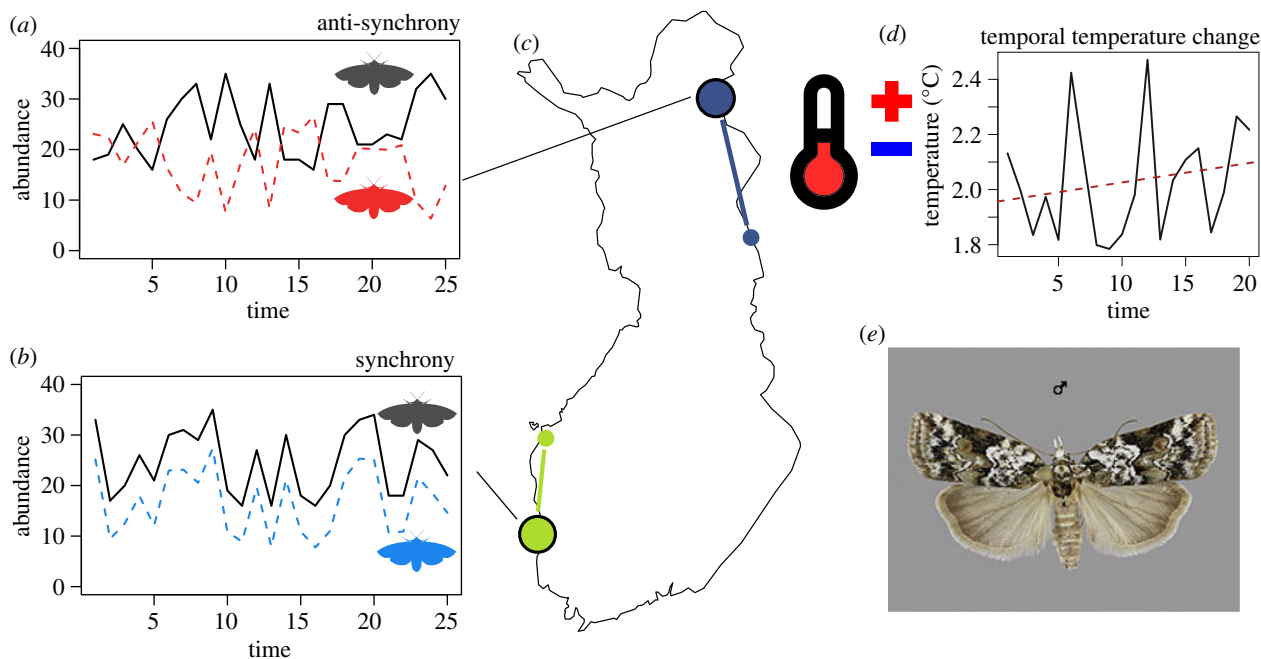


Figure 1. For each shared species between any pair of sites, a time series correlation was calculated. Significant negative and positive correlations ($\alpha = 0.05$)—corresponding to anti-synchronous (a) and synchronous (b) dynamics—were averaged across shared species between pairs of sites in order to quantify link strength. This created one synchrony and one anti-synchrony network, which were combined to create a single synchrony network spanning the entire country of Finland (c). Site-level synchrony values were then related to estimates of mean and temporal variation in environmental change (d) to understand spatial variation in site-level synchrony. A representative Finnish moth species (*Nycteola degenerana*) is pictured in panel (e). (Online version in colour.)

spatial synchrony estimation. Pairs of sites were not necessarily sampled at the same time, and the temporal overlap between sites may influence the estimation of spatial synchrony, as estimates of synchrony required both species to be sampled at a particular sampling event. To account for this effect, we use the number of sampling events at each site as a covariate in our models (more information given below, and see electronic supplementary material, figure S2). This had no effect on our overall findings. Overall, these data cover all species of Macroheterocera (i.e. macro-moths) and the families Hepialidae and Cossidae, and consist of over 4.12 million individual moths belonging to 731 species.

(b) Quantifying environmental change

Data on monthly mean precipitation and temperature between 1990 and 2013 were obtained from the Finnish Meteorological Institute (an extension of the data from [40]). We measured both the mean values and the temporal change in precipitation and temperature for each 1 km² grid cell for the whole of Finland. Temporal change was quantified using Spearman's correlations of environmental conditions and time to account for non-linear environmental changes over time. This created a gridded map of the temporal change in precipitation and temperature for all of Finland (see electronic supplementary material), and data for each sampling site was extracted from this gridded map.

(c) Geography of synchrony

To examine the contribution of each site to spatial synchrony at the community level, we first calculated time series correlations among all pairs of sites and each sampled moth species (figure 1), following the geography of synchrony approach [7]. We used the annual mean moth abundances at each site, to account for the strong seasonality in moth species dynamics. However, we explore the effect of temporal sampling scale in the electronic supplementary material, finding equivalent results when using a monthly sampling scale.

Population dynamics may be synchronous (positive correlation) or anti-synchronous (negative correlation). Synchrony between sites was estimated using Pearson's correlation coefficients, where links between sites were only considered if they were significantly ($\alpha < 0.05$) different from zero. This addresses potential issues of phase-locking and cyclic dynamics, as sites undergoing strong coupled interactions like phase-locking would have a strongly positive relationship. Further, we removed one species known to dominate communities in terms of abundance during certain years in the more northern sites, which is known to exhibit multi-annual population cycles, and found no change to our results (see electronic supplementary material, section entitled 'Removal of a known cyclic species'). Any pair of sites will have a number of time series correlations equal to the number of shared species between sites. To quantify average synchrony between any two sets of sites, we separated the positive and negative synchrony values into two networks, combining species-level networks by taking the mean time series correlation for all shared species between any pair of sites as a measure of positive or negative synchrony. This produced two networks: a synchrony network containing positive mean associations between sites, and an anti-synchrony network containing negative mean associations. We considered the absolute value of the correlation coefficient between pairs of sites as a measure of spatial synchrony. These networks were analysed separately, then site-level contributions to synchrony (anti-synchrony) were combined to estimate overall contribution of a site to spatial synchrony.

To estimate the contribution of each sampling site to synchrony (and anti-synchrony) networks, we calculated two centrality indices, which measure the topological importance of a site in the spatial network based on the number and weights of the associations between sites. The site-level contribution to the network was estimated as the difference between the centrality values in the synchrony network and the anti-synchrony network.

The two measures we used were strength (also referred to as weighted degree centrality) and eigenvector centrality. Strength

was estimated as the sum of link strength (i.e. mean synchrony between a pair of sites) for each site standardized by dividing the total number of links with other sites [41]. We remove this standardization by the total number of links with other sites in the electronic supplementary material, finding that it does not influence our results. Eigenvector centrality is a related measure which uses information on the entire network structure to estimate importance of each node in the network. This approach is used by Google's PageRank algorithm, which quantifies the importance of a node as a function of connections with other important nodes. While often related (see electronic supplementary material), the two measures incorporate different levels of information, and therefore can estimate different aspects of site importance in the synchrony networks. That is, strength captures the importance of a site given immediate local connections, while eigenvector centrality measures the importance of a site based on the connections of those local connections [42,43], providing a more regional estimate of site importance which considers connections across the entire spatial synchrony network.

There are many factors which may influence these centrality measures. Depending on the distribution of synchrony values, sites sharing more species may have higher mean synchrony values on average. This would make synchrony values sensitive to the number of shared species between two sites, or to variation in sampling effort. To address these effects, we considered the association between sites to be the mean synchrony or anti-synchrony value for all shared species, standardized estimates of site importance (centrality) by the total number of synchronous or anti-synchronous links (i.e. the number of other sites each site had significant synchronous or anti-synchronous associations with; see electronic supplementary material), and incorporated sampling effort into our models (as described below).

(d) Relating synchrony to environmental change

The importance of sites to spatial synchrony may be associated with environmental conditions. We used linear mixed-effects models—specifically the R package lme4 [44]—to relate site-level contribution to spatial synchrony (centrality values) to both the mean and temporal variation in precipitation and temperature. Spatial autocorrelation was controlled by incorporating a Gaussian spatial correlation random effect. Some sites were not sampled at each sampling event, due to severe weather conditions or other logistical challenges. This variation in sampling effort may influence the resulting synchrony values and corresponding site-level centrality values. To examine the importance of this effect on site-level centrality, we incorporated the number of sampling events as a fixed effect. This results in two models, depending on whether site-level contributions to spatial synchrony were quantified using strength or eigenvector centrality.

Data and code to reproduce the analyses described are provided at <https://doi.org/10.6084/m9.figshare.9036941>.

3. Results

(a) Synchrony networks

Across our 65 sampling sites, we calculated pairwise synchrony for every possible combination of sites, building up networks of spatial synchrony. Each link in the network was defined as the mean synchrony for all species shared between the two sites. From this, we created two spatial networks, one containing significant ($\alpha = 0.05$) positive mean associations between pairs of sampling sites, and the other containing the significant negative mean synchrony values (electronic supplementary material, figure S1).

Centrality values for each node in the synchrony network provided estimates of site-level contributions to spatial synchrony. We find similar spatial patterns in site importance to synchrony for both centrality measures considered (strength and eigenvector centrality), where more northern sites contributed more strongly to spatial synchrony compared to more southern sites (figure 2). Defining the contribution of each site to synchrony without standardizing by the number of links did not change our overall findings (see electronic supplementary material). Finally, we examined the relationship between site contributions to synchrony and anti-synchrony in the electronic supplementary material, finding that sites contributing strongly to spatial synchrony also contribute strongly to anti-synchrony. This effect may be a function of species richness, but this does not influence our estimates of site-level contributions to overall synchrony, as these values are standardizing by the number of significant correlations linking sites (see electronic supplementary material).

(b) Relating synchrony to environmental change

Northern sites contributed more strongly to spatial synchrony, which might be expected if the spatial distribution of sampling sites was higher in northern latitudes, as synchrony is expected to be greater when distance between sites is small (see electronic supplementary material for exploration of distance decay in synchrony). However, we observe the opposite pattern, with the far more spatially distinct northern sites contributing more strongly to synchrony. Relating the mean values in temperature and precipitation to site synchrony estimates showed that both were negatively related to site-level contributions to spatial synchrony (table 1).

Additionally, site-level contributions to the synchrony network (figure 2) were positively related to temporal temperature change, but unrelated to precipitation change (table 2). This means that sites with lower mean temperature and larger temporal temperature change contribute more strongly to spatial synchrony (figure 2 and tables 1 and 2). Both mean values and temporal variation in climatic conditions were negatively related to one another for both temperature ($r = -0.67$, $t = -7.16$, $p < 0.0001$) and precipitation ($r = -0.32$, $t = -2.68$, $p = 0.009$), suggesting that warmer and wetter sites correspond to low rates of temporal climatic change. We failed to observe a significant effect of variation in sampling effort among sites (table 2), though sampling effort was significantly related to site-level contributions to synchrony in models including mean temperature and precipitation (table 1). Finally, our results were robust to the quantification of pairwise links between sites estimated using all species correlation coefficients instead of only significant relationships (see electronic supplementary material). Specifically, the importance of mean temperature to site-level estimates of synchrony remained similar (electronic supplementary material, table S9), but the influence of precipitation was not observed in the mean climate models. We discuss this difference further in the electronic supplementary material.

4. Discussion

We found clear spatial signals in the importance of sampling sites to spatial synchrony across a large latitudinal gradient,

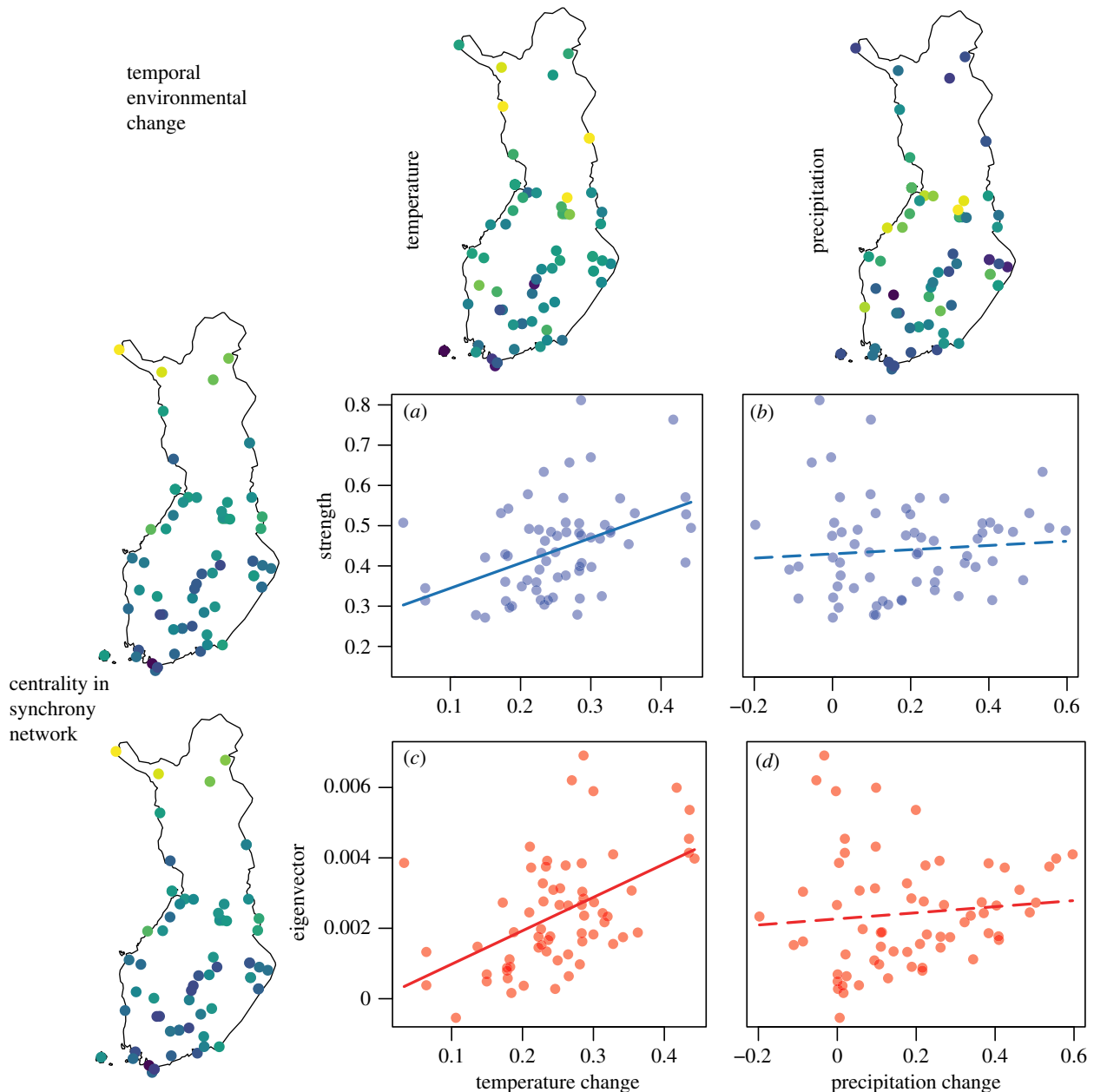


Figure 2. Site-level contributions to the synchrony network in terms of (a,b) strength and (c,d) eigenvector centrality, as a function of temporal change in temperature and precipitation. Maps show the spatial distribution of centrality estimates and temporal change in temperature and precipitation, with warmer (more yellow) colors indicating larger values. Solid plotted lines indicate significant relationships between site-level contributions to the synchrony network and temporal patterns in temperature change, while dotted lines indicate non-significant relationships. (Online version in colour.)

with higher site-level synchrony values in more northern sites. Further, we found a clear relationship between the importance of each site in the spatial synchrony network and (1) mean temperature and precipitation and (2) the temporal change in temperature. This suggests that environmental forcing is potentially an underlying mechanism in synchronizing moth population dynamics, and that the unequal spatial distribution of environmental change is disproportionately influencing spatial synchrony of certain areas. Overall, colder and drier sites tend to contribute more strongly to spatial synchrony, linking mean environmental conditions to synchrony estimates. Further, differences in the temperature change may manifest as differences in the importance of sites to promoting spatial synchrony. Together, our results provide a clear demonstration that gradients in temporal change in temperature, but not precipitation, were related to differences in the relative importance of sites to spatial synchrony. Understanding

which environmental variables are important to driving spatial synchrony—and the associated rates of change in environmental variables—can provide a clearer understanding of the relative importance of dispersal processes and environmental forcing on spatial synchrony. Finally, identifying which sites contribute most to spatial synchrony—a phenomenon closely related to metapopulation persistence—may aid in conservation and management efforts [7], as manipulating the system to reduce spatial synchrony may serve to stabilize metapopulation dynamics.

The approach of examining spatial synchrony networks does not allow us to readily tease apart the relative roles of environmental forcing from the effects of dispersal or predator distributions. Still, it seems unlikely—though not impossible [22,23]—that a mobile predator could be driving the observed dynamics due to the large spatial extent of the study. However, large-ranging migratory bird species that prey on moths could

Table 1. Linear mixed-effects models examining the effects of mean temperature and precipitation on two measures of centrality—strength (marginal $R^2 = 0.53$) and eigenvector (marginal $R^2 = 0.58$)—which estimate the importance of a given site to mean synchrony in moth populations. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

centrality measure	variable	estimate	s.e.	d.f.	t	p
strength	mean precipitation	− 0.007	0.002	61	− 3.08	0.0031
	mean temperature	− 0.043	0.007	61	− 6.22	<0.0001
	sampling effort	0.001	0.0004	61	2.09	0.0410
eigenvector	mean precipitation	− 0.0001	2.3×10^{-5}	61	− 3.29	0.0017
	mean temperature	− 0.0005	7.3×10^{-5}	61	− 7.07	<0.0001
	sampling effort	1.2×10^{-5}	4.3×10^{-6}	61	2.84	0.0061

Table 2. Linear mixed-effects models examining the effects of temporal change in temperature and precipitation on two measures of centrality—strength (marginal $R^2 = 0.20$) and eigenvector (marginal $R^2 = 0.21$)—which estimate the importance of a given site to mean synchrony in moth populations. Synchrony estimates were standardized by the number of significant synchrony links between sites. A spatial random effect was included as a Gaussian spatial correlation, and the number of unique sampling events at each site was included as a fixed effect as a measure of sampling effort.

centrality measure	variable	estimate	s.e.	d.f.	t	p
strength	precipitation	0.025	0.076	61	0.32	0.7483
	temperature	0.587	0.178	61	3.31	0.0016
	sampling effort	− 0.0002	0.001	61	− 0.47	0.6416
eigenvector	precipitation	0.0001	0.0005	61	0.09	0.9295
	temperature	0.007	0.002	61	3.57	0.0007
	sampling effort	$− 5.2 \times 10^{-7}$	5.7×10^{-6}	61	− 0.10	0.9243

have geographical ranges covering large portions of Finland. Moreover, it seems unlikely that dispersal would be a driver in this case, as a higher degree of synchrony was observed in more northern sites, where distances between sites are larger and dispersal becomes less likely. Further, synchrony was observed between sites at the latitudinal extremes of Finland, spanning a greater distance than dispersal processes would be likely to influence. Seasonality in moth communities is pronounced, which could produce signals of synchrony as a function of environmental processes (a form of the Moran effect). These short-term seasonality-driven dynamics capture life history variation and phenological events in moth populations, but are perhaps not the appropriate scale for examining spatial synchrony in longer term data. We examined synchrony at the annual time scale in order to remove transient or seasonal population processes. In the electronic supplementary material (tables S1 and S3), we analyse moth communities at the monthly time scale, finding qualitatively similar results to the annual time scale. It should be noted that the annual scale does not remove multi-year cyclic behavior, as has been observed in a small number of moth species [37,45,46], particularly *Epirrita autumnata* (see electronic supplementary material for an analysis where we remove this species).

Previous work on this cyclic Fennoscandian moth species (*Epirrita autumnata*) suggested the existence of spatial clusters of synchrony [45]. Such work has focused on understanding the cyclic nature of outbreaks, as large increases in population size can defoliate an area. Taking this further, a set of synchronous moth populations may cause synchronous

defoliation across much larger areas, resulting in pronounced effects on forest dynamics [35,47]. Taking a bottom-up perspective, synchrony in the emergence or abundance of a resource may drive synchronous dynamics in the predator species [48]. Relatedly, numerically dominant outbreaking species may drive synchrony by disrupting community dynamics and promoting synchrony in other species through competitive interactions [49,50]. Both of these are potential explanations for the latitudinal variation observed in the importance of each site to the synchrony network, as resource availability and community composition changes with latitude in Finland [51]. Disentangling the relative roles of temporal temperature patterns and the role of resource communities is well beyond the scope of the current work, but disentangling the underlying mechanisms driving geographic variation in site-level contributions to synchrony is an important next step. Another clear next step is the continued integration of graph theoretic approaches to networks of spatial synchrony. Measures of entire networks, instead of each node (habitat patch), may provide insight into the organization of modular subcommunities within synchrony networks, or other interesting network structures. Using the geography of synchrony approach, and comparing spatial synchrony networks of different taxa, may allow inference into the relative roles of dispersal processes, synchronized resources, environmental forcing and the influence of mobile predators or parasites.

In addition to elucidating the underlying mechanisms driving spatial synchrony, our results highlight that we must consider the rate at which environments are changing,

and the spatial distribution of environmental change, as this will certainly influence relative importance of sites to synchrony networks [52]. The significant relationship between the mean and temporal variation in climatic conditions highlights the difficulty in establishing a causal link between synchrony estimates and climatic conditions. It is of great interest that warmer sites contribute less to synchrony networks compared with cold sites, but that these more northern, colder sites are also becoming warmer at an accelerated rate relative to more southern sites (electronic supplementary material, figure S7). Here, we provide a clear demonstration that temporal temperature change over the last 20 years is strongly related to spatial synchrony in moth communities, with sites in areas of greater environmental change (specifically areas warming quicker) contributing strongly to spatial synchrony. The increase in spatial synchrony driven by temporal change in environmental conditions suggests that environmental change may relate to metapopulation extinction risk [6]. Understanding the spatial distribution of the rate of environmental change and identifying the important environmental drivers of

synchrony—scaling from single sites to entire metapopulations—is therefore an important research need. Given that rates of climate change are expected not only to continue but to accelerate, and even more so for higher latitudes, environmental forcing is likely to strongly affect synchrony networks in the future, potentially impacting community structure and demographic processes.

Data accessibility. Data and R code are available on figshare at <https://doi.org/10.6084/m9.figshare.9036941>.

Authors' contributions. T.A.D. and L.H.A. designed the analysis. J.P. and R.L. coordinated the data collection. T.A.D. analysed the data. All authors contributed to manuscript writing.

Competing interests. The authors have no conflicts of interest to declare.

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