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Using geography to infer the importance of dispersal for the synchrony of freshwater plankton

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Spatial synchrony in population dynamics is a ubiquitous ecological phenomenon that can result from predator–prey interactions, synchronized environmental variation (Moran effects), or dispersal. Of these, dispersal historically has been the least well studied in natural systems, partly because of the difficulty in quantifying dispersal in situ. We hypothesized that dispersal routes of plankton were based on the major and consistent water current movements in Kentucky Lake, a large reservoir in western Kentucky, USA. Then, using 26-year time series collected at 16 locations, we used matrix regression techniques to test whether spatial heterogeneity in strengths of hypothesized dispersal predicted spatial patterns of synchrony of phytoplankton and zooplankton, thereby testing for evidence of dispersal as a possible mechanism of synchrony in this system. Nearly all taxa showed significant spatial synchrony that did not decline with increasing linear distance between locations. All taxa also showed substantial geographic structure in synchrony that was not explained by linear distance. Matrix regression revealed that our hypothesized matrix of dispersal pathways, which differed substantially from linear distance, was a significant predictor of spatial variability in synchrony in phytoplankton biomass, and *Bosmina longirostris* and *Daphnia lumholtzi* densities. Thus dispersal was a likely mechanism of synchrony for these taxa. Our hypothesized dispersal matrix was a significant predictor of spatial patterns of synchrony for these taxa even after accounting for numerous alternative possible mechanisms, including possible Moran effects through any of ten physical/abiotic constraints. Our findings indicate that statistically comparing hypothesized or measured dispersal pathway information to synchrony data via matrix regressions can provide valuable evidence for the importance of dispersal as a mechanism of spatial synchrony.

Understanding the mechanisms of spatiotemporal variability in population densities has been a longstanding goal in ecology. Spatial synchrony, a ubiquitous aspect of spatiotemporal population variability, is defined as correlations in the fluctuations through time of the densities of populations in different places. Spatial synchrony is an important phenomenon that has been widely studied (reviewed by Liebhold et al. 2004). Three primary mechanisms of synchrony have emerged from a large body of theoretical and empirical work: dispersal, interactions with a synchronized or mobile species, and environmental fluctuations which are spatially correlated across the landscape (called Moran effects) (Moran 1953, Bjørnstad et al. 1999, Liebhold et al. 2004). These mechanisms can induce population synchrony over a range of spatial scales, the strength of which typically declines as the distance increases between sampled populations (Koenig 1999). Synchrony may sometimes have conservation implications because synchronized metapopulations are thought to be at greater risk because all populations tend to be simultaneously low (Heino et al. 1997, Earn et al. 2000). For this and other applied and basic-science reasons (Liebhold et al. 2004), identifying causal factors that induce and shape synchrony is important.

Despite the ubiquity of spatial synchrony and the common acceptance of the three general mechanisms leading to it, many aspects of spatial synchrony remain poorly understood. For instance, evaluating the relative importance of mechanisms causing synchrony in any given metapopulation is still often difficult. This is true in part because all three mechanisms can generate similar patterns of synchrony, as measured using the most common statistical approaches (Ranta et al. 1995, Kendall et al. 2000, Abbott 2007). Further, determining which mechanism is operating typically requires data on multiple putative drivers of synchrony, i.e. data pertaining to the three mechanisms outlined above. It is rare that data on all three mechanisms, particularly dispersal data, coincides with measurements of the focal taxon.

Theoretical and experimental investigations of dispersal as a synchronizing agent are common, with many studies showing that it can have a strong influence (Ranta et al. 1995, 1998, Kendall et al. 2000, Holland and Hastings 2008, Vasseur and Fox 2009, Vogwill et al. 2009). However, dispersal is still probably the least well studied mechanism of synchrony in natural systems. Only a handful of studies have directly quantified impacts of dispersal on synchrony in natural populations (Ims and Andreassen 2005, Oliver et al. 2017). In some special systems, one or more mechanisms can be ruled out a priori, allowing for more robust demonstrations of another mechanism. Dispersal is often the excluded mechanism because it is the most difficult to measure (Koenig et al. 1996), or unlikely to be a driver of synchrony. For instance, Grenfell et al. (1998) examined synchrony in sheep on different islands, and Rusak et al. (2008) examined synchrony in zooplankton in different lakes. In both these cases and others (Post and Forchhammer 2004, Haynes et al. 2013), dispersal could not reasonably have been the synchronizing agent because dispersal between the measured populations was very limited or absent; the systems in these studies were selected partly for this reason.

Other studies categorize the "dispersal potential" of several species and take a comparative approach to estimating dispersal effects on synchrony by measuring associations between species' strengths of synchrony and dispersal potentials (insects: Sutcliffe et al. 1996, birds: Paradis et al. 1999, Bellamy et al. 2003). This comparative approach may support the hypothesis that dispersal affects synchrony, but it requires data on multiple related taxa and does not seek to describe in detail how dispersal affects synchrony in any particular species. The approach may not reveal how dispersal functionally influences synchrony, as it does not account for how the landscape facilitates or impedes dispersal and thereby influences spatial patterns of synchrony (Powney et al. 2011, 2012).

The most commonly used statistical approaches for assessing spatial synchrony typically test only for isotropic distance–decay relationships, i.e. the strength of synchrony between two populations is assumed to decline solely or principally as a function of the geographic distance between them, and the rate and nature of this decline is assessed (Bjørnstad et al. 1999, Bjørnstad and Falk 2001). However, recent work suggests that accounting for heterogeneity in landscape or geographic influences, beyond simple distance–decay relationships, may provide additional insight into the mechanisms of synchrony, including dispersal (Powney et al. 2011, 2012, Gouveia et al. 2016, Walter et al. 2017); we here use such a geographic approach to study the influence of dispersal on synchrony in a freshwater plankton system. Standard distance–decay approaches ignore, among other factors (Walter et al. 2017), the potential for spatial heterogeneity in dispersal (or another mechanism) to result in spatial heterogeneity in synchrony, though theoretical simulations have shown that spatial heterogeneity in dispersal can lead to complex spatial patterns of synchrony (Holland and Hastings 2008). Spatially heterogeneous and non-random dispersal have been predicted or observed in many natural systems, and are often attributed to landscape influences (Clobert et al. 2009). Information on the mechanisms that facilitate dispersal, such as water-current, wind, or landscape resistance patterns, can provide information on likely dominant spatial patterns of dispersal. These patterns can be compared statistically to spatial patterns of synchrony to provide evidence for or against the importance of dispersal as a synchronizing mechanism.

Our system in particular is amenable to a geographic approach because it is strongly structured by dominant water flow patterns which are very likely to induce spatially structured patterns of dispersal in plankton. This effectively creates a disconnect between Euclidean distances (i.e. straight-line distance between points) and 'ecologically effective geographic distances' (Michels et al. 2001a): locations in close geographic proximity may have very different ecological dynamics due to isolating barriers between the locations, whereas more geographically distant sites may have similar dynamics due to greater connectedness through habitat corridors or features which facilitate dispersal. Comparisons between hypothesized or measured connectivity metrics, geographic distance, and spatial patterns of synchrony have been carried out, though infrequently, in both aquatic and terrestrial ecosystems (Bunnell et al. 2010, Powney et al. 2012), so our approach builds from previous examples. We believe the approach is a promising one for helping to illuminate dispersal influences on synchrony across a range of systems.

Our study complements the bulk of existing studies of synchrony in freshwater plankton in part because most previous studies have examined synchrony of populations in different water bodies, and we examine synchrony within one large reservoir. Most studies of spatial synchrony of freshwater plankton among different water bodies have supported distance–decay relationships, Moran-effect causes of synchrony, and/or species-specific variability in the strength of synchrony (Magnuson et al. 1990, Rusak et al. 1999, 2008, Vogt et al. 2011, Pandit et al. 2016). Dispersal as a mechanism of synchrony has typically been less of a focus in between-lake synchrony studies because it is unlikely that synchrony would arise from this mechanism between lakes: dispersal between lakes is probably very limited in numbers of organisms transferred. A few studies have investigated synchrony between different locations within a single water body (Lansac-Tôha et al. 2008, Seebens et al. 2013, Lodi et al. 2014), where dispersal via currents could be more important as a synchronizing agent, though dispersal as a mechanism has only rarely been explicitly investigated or compared to alternative possible mechanisms in any freshwater study (Seebens et al. 2013).

We tested for possible effects of heterogeneity in dispersal connectedness on spatial patterns of synchrony of zooplankton taxa and chlorophyll a, an index of phytoplankton biomass, within Kentucky Lake, a large freshwater reservoir in the southeastern USA (Fig. 1). Between-lake zooplankton dispersal has been well studied in the contexts of space (e.g. movement via birds or wind currents) and time (e.g. hatching from resting eggs) (reviewed by Havel and Shurin 2004). Here, we instead consider dispersal to be more relevant via intra-reservoir movement of plankton through water currents. Basic information about the hydrology of the reservoir provided us with a reasonable and compelling a priori hypothesis about dominant patterns of

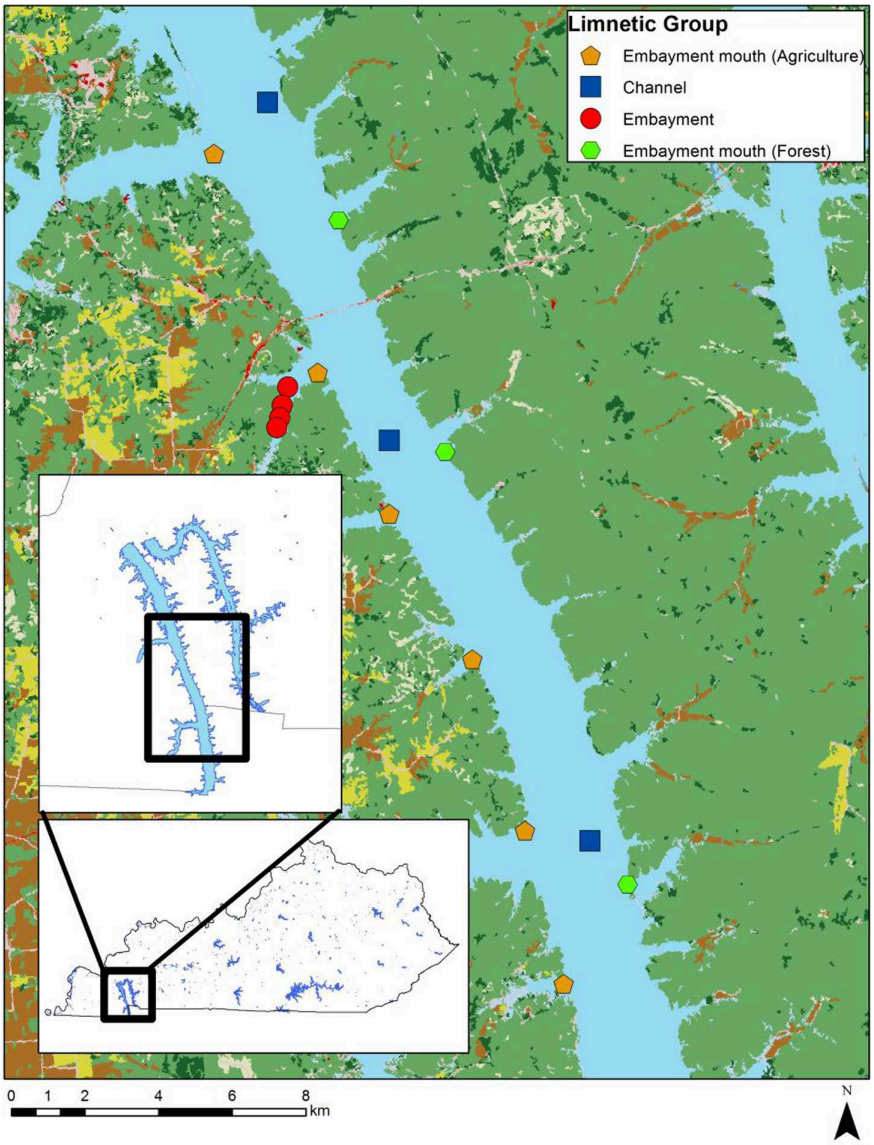

Figure 1. Map of the study area sampled by the Kentucky Lake Monitoring Program on Kentucky Lake, KY, USA. Symbols represent sampling locations monitored from 1990–2015, categorized by limnetic group. Land cover shading indicates deciduous forest (green), evergreen forest (dark green), developed high intensity (red), developed open space (pink), pasture (yellow), cultivated crops (brown), grasslands (tan) and water (blue).

interconnectedness between different sampling locations in the lake: relatively high flow rates within the former river channel that runs down the middle of the reservoir would isolate locations sampled on opposite sides of the reservoir and inhibit upstream movements, limiting dispersal and ultimately affecting patterns of synchrony. Testing the correspondence between these spatially heterogeneous patterns of likely dispersal and spatial patterns of synchrony allowed us to compare hypothesized dispersal to potential alternative synchronizing mechanisms. We not only seek to provide evidence as to whether dispersal is an important agent of synchrony in the Kentucky Lake system; we also illustrate an approach to studying the mechanisms of synchrony that we believe can be broadly useful, in any system with direct measurements of dispersal or with clear habitat structure, to improve understanding of dispersal as a synchronizing mechanism.

Methods

Study site

Kentucky Lake is a large, northward flowing, mainstem reservoir (length ≈ 300 km, width ≈ 2 km, surface area ≈ 650 km^2, mean depth ≈ 6 m) on the Tennessee River in western Kentucky, USA (Fig. 1). Water retention time in the reservoir is very short, averaging < 30 days (Bukaveckas et al. 2002, Yurista et al. 2004), making the reservoir functionally more riverine than lacustrine. As is typical of mainstem impoundments, the deepest part of the reservoir is in the original channel of the Tennessee River (max depth of ≈ 21 m in summer) but much of the inundated surface area is the old flood plain (average depth ≈ 6 m). Water depth varies by approximately 2 m between winter and summer. Water release rates from the dam, about 24 km downstream from

the study sites, average ≈ 40 000 $m^3 s^{-1}$, but are highly dependent on power generation and flood control scenarios. The lake is considered mesotrophic and is vertically well mixed because of currents and wind. These features result in most primary and secondary production being washed through the dam and out of the system (Yurista et al. 2004). The lake does not develop substantial ice cover in the winter, except in the backs of small embayments.

Data collection

We used data from the Kentucky Lake Monitoring Program (KLMP), which was designed to document long-term physiochemical and biotic patterns in a 30 km section of Kentucky Lake (White et al. 2007). KLMP collects samples at multiple sites every 16 days during the spring through fall months and every 32 days during winter months. Here, we focused on a 26-year period of record (1990–2015) for the 16 primary sampling sites. Euclidean distances between sites range from 0.3–25 km (Fig. 1). The 16 locations fall within one of four limnetic habitat types: within an embayment arm on the western shore (n = 4 sites), embayment mouths on the western shore (n = 6 sites), embayment mouths on the eastern shore (n = 3 sites), and main channel sites in the original river bed (n = 3 sites). Embayments on the western shore drain primarily agricultural land, while embayments on the eastern shore drain the primarily forested Land Between the Lakes National Recreation Area. The presence of the channel is the main feature of habitat structure on which we rely for our hypothesized connectivity matrices. We expected sampling locations to be more or less isolated from each other based on their positions relative to the channel and flow patterns (i.e. east versus west sides of the reservoir; upstream versus downstream). We expected connectedness to be substantially unrelated to geographic distance. Detailed information on lake parameters and sampling methodologies of the KLMP is given in Bukaveckas et al. (2002), Yurista et al. (2004), White et al. (2007) and Levine et al. (2014).

Zooplankton samples were collected using a 15 l Schindler–Patalas trap (fitted with a 243 µm sieve) that was lowered to 5 m below the surface or half of the maximum water depth (whichever was shallower) and then retrieved. Three replicate samples were collected at each sampling site on each visit. We summed the total number of individuals of each species across the three replicate samples to estimate total abundance per species for each sampling site on each visit. Zooplankton were enumerated to the finest possible taxonomic resolution for each replicate. For this study, we focused on the nine most abundant taxa: calanoid copepods, cyclopoid copepods, and the cladocerans *Daphnia retrocurva*, *D. lumholtzi, Ceriodaphnia* sp., *Bosmina longirostris*, *Diaphanosoma birgei*, *Holopedium amazonicum* and *Leptodora kindtii*. Copepod counts were totaled by subclass (Calanoida or Cyclopoida); see Williamson and White (2007) for a list of the dominant species in the system in these groups. *Leptodora kindtii* and Cyclopoida are primarily predaceous, Calanoida are primarily omnivorous, and the cladocerans are primarily herbivorous.

We focused on a set of 10 environmental parameters known to be important to phytoplankton and zooplankton dynamics (Yan et al. 2008, Shurin et al. 2010) and that could potentially have produced Moran effects. Water temperature, dissolved oxygen (DO), conductivity and pH were recorded at 1 m intervals throughout the entire water column using a YSI multi-parameter sonde (Yellow Springs Instruments) at each site during each sampling cruise. Water samples for laboratory analyses were collected 1 m below the surface and 1 m above the lake bottom using a 2-l Kemmerer sampler. A subsample of water was filtered through 2.5 cm Whatman GF/C glass fiber filters, and then stored on ice prior to chemical analysis. Chlorophyll a concentrations were determined in water collected 1 m below the surface using acetone extraction and spectrophotometric methods (APHA 1989). Concentrations of silicon dioxide (SiO_2), nitrogen (dissolved and total N), and phosphorus (dissolved and total P) were also determined from near surface and bottom samples. Concentrations of N and P were obtained using Kjeldahl digestion (P and N, 1990–1993), acidic persulfate digestion (P, 1994–2015), and alkaline persulfate digestion (N, 1994–2015). See Bukaveckas et al. (2002) and Yurista et al. (2004) for more detailed descriptions of nutrient analyses. Secchi disk depth was recorded at each sampling site on the shaded side of the sampling vessel using a 20 cm Secchi disk.

Data preparation

Measurements above were used to construct annual time series of mean values for each variable in each sampling location using data from April to November, which approximately coincides with the growing season, the time period of maximum depths of Kentucky Lake, and when KLMP performed sampling at 16-day intervals (Supplementary material Appendix 1 Fig. A1.1–A2.2). We also averaged over all depths for variables that were collected at multiple depths (e.g. data collected from the YSI sonde). Annualizing time series is standard practice in studies of synchrony (Buonaccorsi et al. 2001). Correlation coefficients between locations using sub-annual (e.g. monthly) times series would be very high due solely to the seasonal component in the time series, and would reflect the extent to which phenology and seasonal successional patterns (Sommer et al. 1986) are similar across the lake instead of reflecting patterns of synchrony in multi-annual population fluctuations that we sought to study with the annualized data.

No *D. lumholtzi* and *H. amazonicum* were identified in 1990 and 1996, respectively, though sampling occurred. We used zeros for these species and years. *D. lumholtzi* is an invasive zooplankton that was first documented in Texas in 1990 and spread rapidly throughout the eastern US (Shurin and Havel 2002). The species was detected in Kentucky Lake for the first time in 1991. After data processing, we had complete time series for phytoplankton biomass and all zooplankton taxa. Total N and P had many missing values in 1993, so we replaced missing values by monthly means for the site before computing growing-season averages. We log(x+1)-transformed each variable to normalize the distributions, and then linearly detrended each site's time series for all biotic and abiotic variables to remove any longitudinal trends within the data. Detrending involved regressing transformed abundance against year for each location, extracting the residuals, and then dividing by the standard deviation of

the residuals. Detrending is a standard procedure in studies of synchrony. Correlations between time series can be produced both by related fluctuations and by trends in both time series, but the concept of synchrony is typically not considered to include common trends.

Descriptive analysis

We first provide a descriptive overview of spatial synchrony in the system by calculating nonparametric cross-correlation functions on the transformed and detrended time series using the 'Sncf' function in the 'ncf' package in R (Bjørnstad 2016, <www.r-project.org>). This technique compares synchrony against geographic distance between sites. We used Euclidean, or straight-line, geographic distance as the measured distance between sites for these plots because that has been the typical choice in studies of synchrony. For most pairwise comparisons, the straight-line distance is equivalent to the water distance (Fig. 1), though as we explore further below, not equivalent in effective geographic distance based on connectivity.

Main analysis

Our principal statistical analyses used matrix regression methods (Lichstein 2007, Haynes et al. 2013). Matrix regression is similar to partial Mantel tests, where the predictive significance of multiple individual covariates (matrices) is assessed on a response matrix using linear regression. Matrices represent pairwise comparisons between sampling locations, so all matrices are 16 × 16, for our 16 locations. Matrix regression is conceptually similar to standard linear regression, but it properly accounts for non-independence of pairwise site comparisons to determine whether sites which are more related to each other, as characterized by one of the predictor matrices, are also significantly more or less related to each other as characterized by the response matrix. Significance was established with permutation procedures using 9999 permutations in all tests. We used matrix regression tools from the 'ecodist' package in R (Goslee and Urban 2007).

Response matrices in all regression models were matrices of pairwise Spearman correlations (lag-0) between the transformed and detrended zooplankton abundance or phytoplankton biomass time series at the 16 sampling sites. Such matrices contain all available information on spatial variability in synchrony measured with correlation, so if a matrix characterizing spatial structure of dispersal connectivity between sites were found to be significantly associated with such a response matrix, after statistically controlling for other possible mechanisms of synchrony, it would provide evidence for dispersal as a mechanism of synchrony. The nine zooplankton taxa and phytoplankton biomass were analyzed separately.

We quantified heterogeneity in dispersal connectivity between sites in our matrix-regression context by generating a dissimilarity matrix. As for all our matrices, rows and columns of the matrix corresponded to sampling sites. The *ij*th entry in the dispersal matrix contained the hypothesized difficulty of dispersing from the *i*th site to the *j*th. The main dispersal assumptions we followed in constructing the matrix were as follows. We assigned a 0 (easy dispersal) to the *ij*th matrix entry when site *j* was downstream of *i* and both locations were in the main channel, and when *i* and *j* were both within the embayment. We assigned 1 (medium dispersal) for *i* and *j* such that plankton would have to move from the side of the lake into the main channel to get to *j*, a downstream site on the same side of the lake. Upstream and cross-channel movements were typically assigned a 2 (difficult dispersal). The matrix is displayed in Supplementary material Appendix 2 Table A2.1. The matrix as constructed so far was not symmetric because moving from up-current sites to down-current sites and vice versa were not equivalent under the rules we applied. However, synchrony is a symmetric phenomenon (the correlation of population dynamics in location A with dynamics in B is the same as the correlation of B with A), and synchrony should depend on overall dispersal connectivity of sites, which will be greater, for instance, for bidirectional dispersal than for unidirectional dispersal. We therefore averaged the dispersal matrix constructed above with its transpose to make a symmetric matrix which characterizes overall between-site connectivity (Supplementary material Appendix 2 Table A2.2). For example, if site A is upstream from B in the main channel, then dispersing from A to B would be assigned a 0, whereas dispersing from B to A would be a 2, resulting in an entry of 1 in the connectivity matrix we used in subsequent analyses. If sites A and C are on opposite sides of the lake, then dispersal is a 2 in both directions, resulting in a connectivity of 2. The symmetric matrix was used in all regressions.

Our connectivity classification focuses on broad, persistent water movement patterns, and likely underestimates actual diversity of water-current dispersal pathways because it ignores smaller currents, eddies, and other potentially circular flow. Lack of systematic and detailed water movement data for Kentucky Lake prohibited the use of more complex features in our representation of connectivity, but nevertheless our matrix is probably a reasonable approximation of relative between-site dispersal connectivity. Our connectivity matrix differed strongly from the matrix of linear distances between sites because cross-channel site pairs could be relatively close together or far apart, as could relatively well-connected channel sites.

We evaluated evidence for dispersal as a mechanism of synchrony while controlling for the potential effects of 14 other covariates representing Moran effects, geographic distance, and two other factors potentially altering synchrony and its spatial structure: limnetic group and mean abundance differences between sites. We represented each of these variables as (dis)similarity matrices between sites. Potential Moran drivers were represented as 10 16 × 16 correlation matrices for 10 different possible drivers of plankton dynamics: water temperature, pH, conductivity, Secchi depth, DO, SiO_2 and dissolved/total N and P. Each matrix was constructed using Spearman correlation coefficients between detrended time series from pairs of sites. We calculated pairwise Euclidean distances between sites to quantify geographic distance.

To partly account for potential unmeasured Moran drivers, we categorized sites based on general limnetic conditions (the limnetic groups of Fig. 1). Limnetic groups capture differences in lake position, depth and hydrology (Lansac-Tôha et al. 2008, Tumolo and Flinn 2017). We constructed

a similarity matrix that consisted of 0s for within-limnetic-group comparisons and 1s for between-group comparisons. We sought to account for the possibility that sites may show stronger synchrony patterns within limnetic groups than between them. This partly controls for the potential effects of unmeasured Moran drivers which were more synchronized within than between limnetic groups.

It is known that differences in the nature of density dependence between sites can influence spatial patterns of synchrony (Liebhold et al. 2006, Walter et al. 2017). To partially control for this possibility, we generated dissimilarity matrices in mean abundance for each zooplankton taxon and for phytoplankton biomass. Time series of zooplankton abundance or phytoplankton biomass were averaged for each site, and absolute pairwise differences in abundance were used to fill the dissimilarity matrices. This was considered an indicator of possible differences in density dependence because it may reflect differences in carrying capacity between sites. This is only a very rough, approximate characterization of potential differences in density dependence, however, and could also represent differential responses of abundance to density-independent factors. The average abundance dissimilarity matrix for each taxon was used in regressions for that taxon's synchrony matrix.

To test whether dispersal may have been a mechanism of synchrony for our zooplankton taxa or for phytoplankton biomass, we first tested whether our dispersal connectivity matrix was, by itself, a significant determinant of spatial patterns of synchrony by regressing each taxon's synchrony matrix against the connectivity matrix. If dispersal showed a significant association with synchrony, we then re-tested for significance of dispersal while controlling for the 14 alternative mechanisms outlined above, to ensure the initial association was not due to alternative mechanisms that had similar spatial configuration to our dispersal matrix. We tested two models for each response by combining the Moran drivers into two groups: physical and nutrient drivers (see below). Separating covariates into two categories in this manner was done to balance the goals of controlling for multiple potentially confounding factors while also not overfitting and thereby obscuring real connectivity–synchrony relationships. In summary, we fitted up to three models for each focal taxon and, in each case, tested for significance of the connectivity matrix:

Dispersal only: Synchrony ~ D_{sp}

Dispersal and Physical: Synchrony ~ $D_{sp}+D_{st}+G_r+D_{ab}$+Temp +Cond+pH+DO+Secchi

Dispersal and Nutrient: Synchrony ~ $D_{sp}+D_{st}+G_r+D_{ab}+N_{tot}$ $+P_{tot}+N_{dis}+P_{dis}+SiO_2$

Here D_{sp} is the dispersal connectivity matrix, D_{st} is the Euclidean distance matrix, G_r is the limnetic group matrix, D_{ab} is the dissimilarity matrix of average abundance of the focal taxon, and Temp, Cond, pH, DO, Secchi, N_{tot}, P_{tot}, N_{dis}, P_{dis} and SiO_2 are correlation matrices for time series of water temperature, specific conductance, pH, dissolved oxygen, Secchi depth, total nitrogen, total phosphorous, dissolved nitrogen, dissolved phosphorous and silicon dioxide. If the dispersal term was significant after controlling for these factors, we concluded that our connectivity matrix was an important determinant of spatial variation in synchrony, and therefore that dispersal was probably an important factor causing synchrony (Haynes et al. 2013). We tested for but did not find evidence of multicollinearity among variables (variance inflation factors < 3.3). We also combined the environmental drivers with principle components analysis (Haynes et al. 2013), and tested for the importance of our dispersal matrix as a determinant of synchrony while controlling for synchrony in the first and second principle components axes, which explained 45% of the variation in environmental drivers. Results were similar to those described below, so are not shown.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.21jt3> (Anderson et al. 2017).

Results

All variables, both biotic and abiotic, showed high levels of spatial synchrony that decayed little or not at all with geographic distance (Fig. 2; Supplementary material Appendix 3 Fig. A3.1). There was still a substantial amount of unexplained variability in synchrony after accounting for geographic distance between sampling locations, and this is apparent when the raw values of synchrony are visualized against geographic distance (Fig. 2) and is indicative of spatial structure beyond linear distance decay. Mean pairwise cross correlation coefficients ranged from 0.35 to 0.77 for zooplankton abundance and phytoplankton biomass, and 0.49 to 0.94 for environmental variables. It is evident by comparing colors on Fig. 2 to Euclidean distances on the horizontal axes that our dispersal connectivity estimates differed substantially from Euclidean distance. In some cases dispersal connectivity appeared visually likely to help explain synchrony (e.g. Fig. 2a), though only statistical testing as described in methods will reveal whether this visual impression corresponds to a significant result.

In the dispersal-only models, the dispersal connectivity matrix was a significant predictor for four of the ten taxa: phytoplankton biomass, *Bosmina longirostris*, *Daphnia retrocurva* and *Daphnia lumholtzi*. The amount of variation (R^2) explained ranged widely among these taxa, spanning from 10% to 44% (Table 1). The parameter estimates for dispersal were all negative (Table 1), indicating synchrony declined as the movement difficulty between sites increased (Fig. 3). The dispersal connectivity matrix was not significant for *Diaphanosoma birgei*, *Holopedium amazonicum*, *Ceriodaphnia* sp., *Leptodora kindtii* and both copepod groups.

Dispersal connectivity was significant for phytoplankton biomass, *Bosmina longirostris* and *Daphnia lumholtzi* after controlling for either set of Moran variables (Table 1). The dispersal term was only marginally significant for *Daphnia retrocurva* in the nutrient model, and not significant in the physical model (Table 1). The amount of variation explained by each of the two full models that included the different Moran drivers ranged from 40% to 56% in the physical Moran model and 29% to 63% in the nutrient Moran model (Table 1). As with the dispersal-only models, the parameter estimates for dispersal were always negative (Table 1),

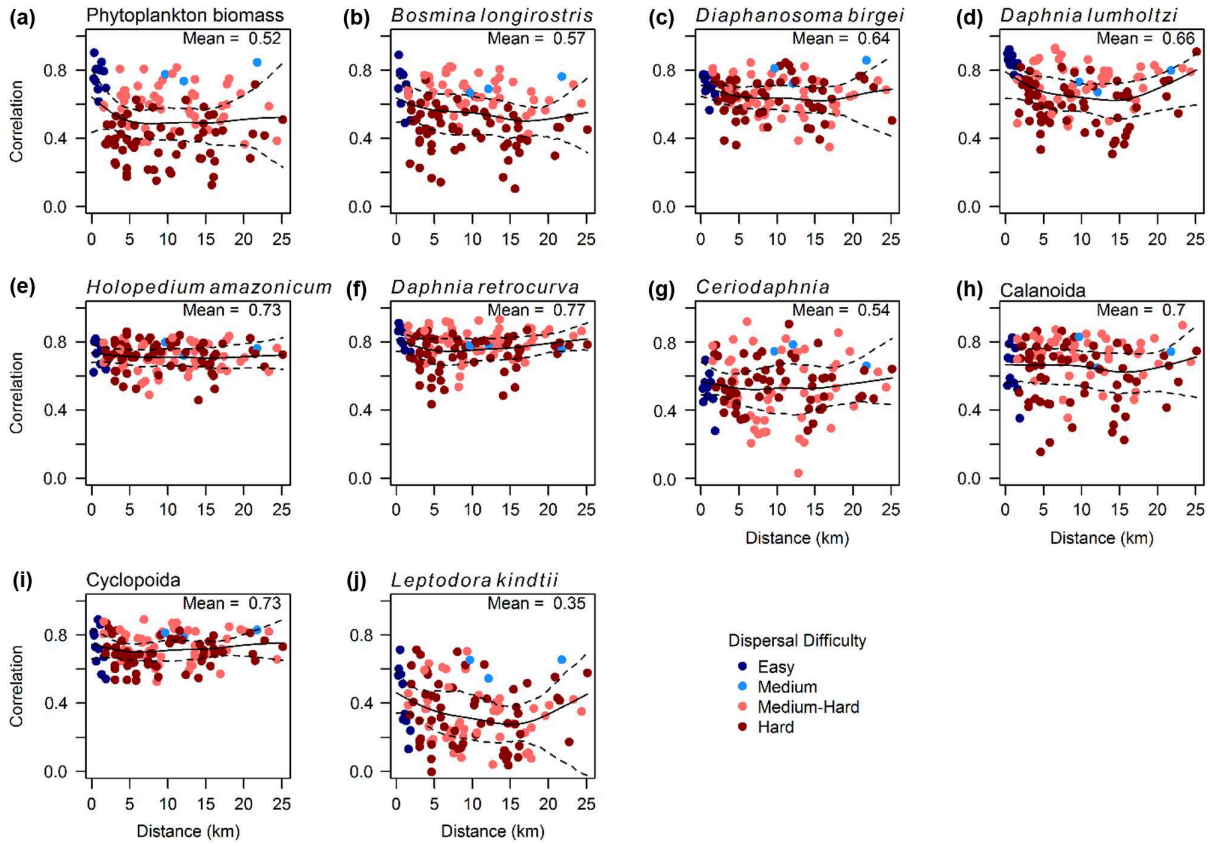

Figure 2. Non-parametric cross correlation functions for zooplankton abundance and phytoplankton biomass time series. Distance used on the horizontal axis is Euclidean distance between sites. Points are Spearman correlations between sampling locations and are colored by dispersal difficulty: dark blue = easy dispersal/high connectivity (dispersal connectivity matrix value 0), light blue = medium difficulty (1), light red = medium-hard difficulty (1.5), and dark red = hard dispersal/low connectivity (2). The solid line is the spline fit. Dashed lines are 95% confidence envelopes of the spline fit, and the mean correlation between all pairs of sites is at the top.

meaning increasing dispersal difficulty between sites reduced observed synchrony between sites, as expected if dispersal is a true cause of synchrony. We note that, in Fig. 2, dispersal connectivity (color), not geographic distance, was visibly associated with synchrony for phytoplankton biomass, *Bosmina longirostris* and *Daphnia lumholtzi*.

Discussion

Several mechanisms have the capacity to generate spatial synchrony among separate populations, including synchronous environmental drivers, interactions with synchronized or mobile species, and dispersal (Liebhold et al. 2004). Historically, dispersal has been the most difficult synchronizing mechanism to identify and study in natural populations because of difficulties associated with quantifying movements among populations. In fact, rather than addressing the importance of dispersal, many researchers have focused instead on systems where it is absent as a confounding factor of other patterns and causes of synchrony (Grenfell et al. 1998, Post and Forchhammer 2004). In our study, we instead created a reasonable hypothesis about the routes and relative strengths by which dispersal (operating in our system via water currents that facilitate or impede movement) should transport plankton around Kentucky Lake, and we tested the compound hypothesis that dispersal was an important synchronizer and the hypothesized dispersal matrix was an adequate parameterization of relative connectivity of each site with other sites. We found that our

Table 1. Estimates of the dispersal coefficient (Est.), the p-values for the significance of the dispersal term (P) and the overall model R^2 for each of the three models: dispersal-only; dispersal plus the physical Moran effects plus geographic distance, limnetic group and density dependence; and dispersal plus nutrient concentration Moran effects plus geographic distance, limnetic group and mean abundance. p-values are for the dispersal term only, not for the significance of the whole model. See text for details.

	Dispersal only			Physical Moran			Nutrient Moran		
Species	Est.	p	R^2	Est.	p	R^2	Est.	p	R^2
Bosmina longirostris	–0.16	**0.001**	0.25	–0.09	**0.02**	0.44	–0.13	**0.002**	0.38
Chlorophyll a	–0.21	**0.001**	0.44	–0.17	**0.0001**	0.56	–0.17	**0.0001**	0.63
Daphnia lumholtzi	–0.13	**0.001**	0.26	–0.07	**0.03**	0.45	–0.11	**0.0008**	0.37
Daphnia retrocurva	–0.06	**0.011**	0.10	–0.02	0.55	0.40	–0.05	0.05	0.29

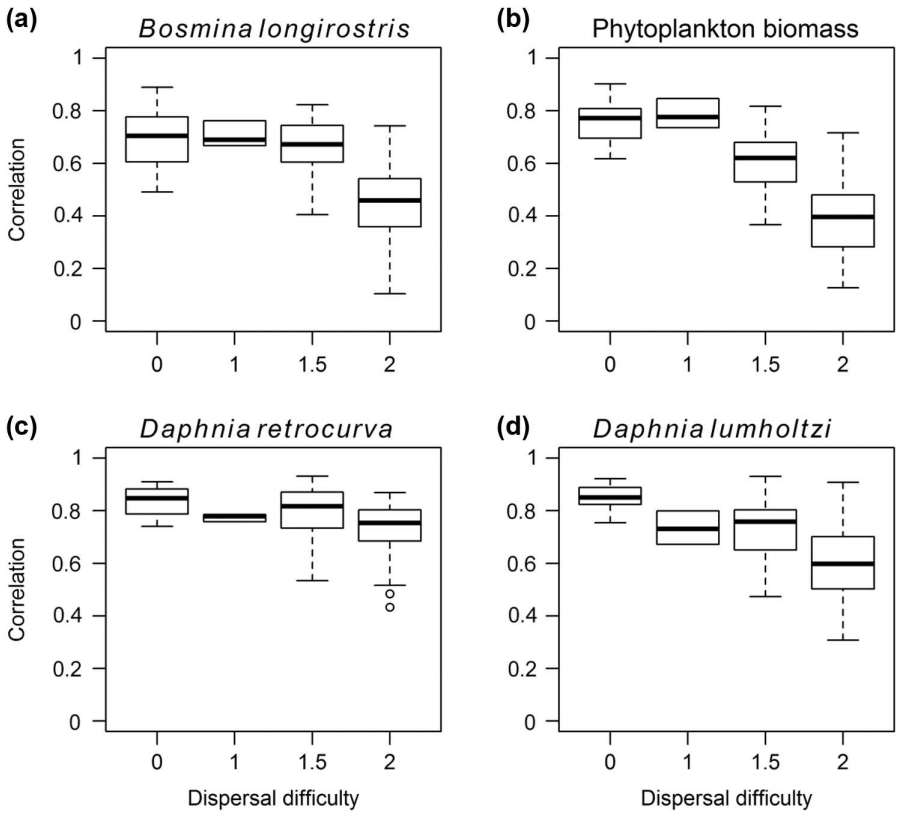

Figure 3. Spatial synchrony of taxa where dispersal was a significant predictor variable by itself in the dispersal-only models. The horizontal axis shows the degree of dispersal difficulty among sites, with higher numbers representing greater difficulty. Significance remained for A, B and D after controlling for differences in mean abundance, limnetic group effects, geographic distance, and ten different Moran drivers (Table 1).

dispersal matrix was a significant predictor of geographic patterns of synchrony for two zooplankton species and phytoplankton biomass over the spatial scale of our study area, even after controlling for 14 alternative mechanisms, such as Moran effects. Our models explained up to 63% of the variance across pairs of sites in spatial synchrony. This is a notable success given that matrix regression techniques often yield lower R^2-values than standard regression (Mortelliti et al. 2015). Therefore, dispersal was likely at least one of the causes of synchrony for these taxa across our study area. Our results represent one of few observational studies with concrete evidence that dispersal is an important determinant of synchrony (Bunnell et al. 2010, Powney et al. 2012, Oliver et al. 2017), complementing other indirect evidence obtained by comparing species with different dispersal abilities (Sutcliffe et al. 1996, Paradis et al. 1999).

There are two reasons our approach provides evidence rather than certainty that dispersal is a mechanism of synchrony, but nevertheless we argue that the evidence provided is persuasive and valuable, and that our approach can usefully be applied to a range of other systems. First, the spatial dispersal connectivity patterns we compare to patterns of synchrony comprise only a hypothesis about dominant movement tendencies, based on knowledge of system hydrology. But in systems such as ours that have clear and strong habitat structure (i.e. directional flow and the channel that divides locations), hypotheses about dispersal patterns seem quite reasonable. Such hypothesized connectivity information is likely to be much more widely available for other systems than are direct and comprehensive dispersal measurements, which are notoriously difficult to obtain. Approaches like ours have already been successful in terrestrial systems (Powney et al. 2011, 2012). Second, we can never completely eliminate the possibility that our hypothesized dispersal connectivity matrix mirrors the spatial pattern of an unmeasured Moran driver or other mechanism of synchrony that is actually the cause of observed spatial patterns of synchrony. But this possibility is unlikely, in our view, because: we have statistically controlled for a large number of alternative possible mechanisms of synchrony; we used limnetic groups in an effort to partially control for additional unmeasured Moran drivers; the likelihood of obtaining our significant results if dispersal were not actually a mechanism of synchrony is low (i.e. our p-values are low, Table 1); we obtained significant results for three of 10 taxa, whereas type-1 errors alone would yield an expected 0 or 1 significant results; and model coefficient signs are consistent with the expected direction of dispersal effects on synchrony. The dispersal connectivity matrix was significantly associated with synchrony of a few abiotic variables (Supplementary material Appendix 4), which a priori could also have contributed to synchrony in our focal taxa. But because we statistically controlled for these variables in our tests of the importance of dispersal for synchrony, this fact does not undermine the importance of dispersal.

Our study highlights a system in which geography had a strong influence on synchrony, but via geographic patterns that were markedly distinct from simple Euclidean distance, making our results an example of anisotropic synchrony (Bjørnstad et al. 1999). This finding is visually apparent in Fig. 1a, b, d: pairs of locations with different dispersal difficulties clearly separate vertically, although such sites could be geographically close or distant. Sites across the channel in Kentucky Lake were geographically close but probably less accessible because of the channel, and were also relatively unsynchronized for phytoplankton biomass, *Bosmina longirostris* and *Daphnia lumholtzi*. Thus, direction between sites (cross channel versus along channel) matters for determining the strength of synchrony, rather than distance being the only factor; a dependence on direction is what defines anisotropy (Bjørnstad et al. 1999).

Systems with certain features are probably the best candidates for our approach to studying dispersal as a mechanism of synchrony. The habitat structure in our system was centered on the main channel as a dispersal barrier, but knowledge of habitat structure in the form of especially 'permeable' corridors that promote movements between populations has also been used to enhance understanding of dispersal effects on spatial synchrony (Powney et al. 2012, Oliver et al. 2017). We speculate that other systems where dispersal is highly directional or otherwise structured, such as other streams/rivers or systems with wind-dispersed plants, or systems in which use of corridors is likely, would provide additional useful information on the importance and nature of dispersal as a cause of synchrony in the natural world. Several riverine studies have been conducted on spatial synchrony, but have found either limited evidence of synchrony (Cattanéo et al. 2003), or have concluded that dispersal-induced synchrony was unlikely, as synchrony patterns did not decline with distance, a previously hypothesized requisite of dispersal (Ranta et al. 1995, Grenouillet et al. 2001). However, none of these previous river studies of spatial synchrony included detailed measures or hypotheses of population connectivity in their analysis, or examined spatial heterogeneity of dispersal or synchrony. These studies therefore may have falsely concluded that dispersal was unimportant because they assumed the strength of dispersive connections between sites was correlated with distance between sites, and we have argued that in river-like systems such as Kentucky Lake, this need not be the case for planktonic or weakly swimming organisms.

Our approach essentially assumes that in real systems for which dispersal is an important mechanism of synchrony, pairs of locations that are better connected by dispersal will tend to be more synchronized. This is a reasonable assumption, and was borne out in our system, but there may also be a need to explore whether indirect dispersal connections can alter this picture. Holland and Hastings (2008) performed theoretical simulations of spatially extended predator–prey systems, showing that spatial dispersal connectivity networks can relate in complex ways to spatial patterns of synchrony, at least for the idealized deterministic model they considered. It seems possible, a priori, that strong indirect dispersal connectivity between sites A and B may sometimes produce greater synchrony than would direct dispersal. For instance, if strong dispersal occurs between A and several sites $C_1, \ldots, C_n$, and also between B and the same sites, synchrony between A and B may be stronger than if A and B were directly but weakly connected. Additional theoretical study of expected relationships between dispersal networks and synchrony networks that considers the role of indirect connections may be warranted.

The reason why dispersal appeared to be the mechanism of synchrony for phytoplankton biomass, *Bosmina longirostris* and *Daphnia lumholtzi* but not for our other taxa is unknown. One possible explanation is taxonomic differences in swimming abilities: good swimmers, which may tend to be larger, may be less affected by flow patterns and correspondingly their spatial patterns of synchrony should be less related to our flow-based dispersal matrix. Phytoplankton biomass and *Bosmina longirostris* are both small-bodied (Culver et al. 1985) and have no-to-poor swimming abilities (Jack et al. 2006). Correspondingly, our dispersal connectivity matrix alone explained a large fraction of the spatial variation in synchrony for these taxa (phytoplankton biomass: 44%; *B. longirostris*: 25%; Table 1). However, *Ceriodaphnia* sp. and *Diaphanosoma birgei* are also small-bodied zooplankton (Culver et al. 1985), and we detected no association between dispersal connectivity and synchrony. Furthermore, *Daphnia lumholtzi* is a larger-bodied species but showed a strong association between connectivity and synchrony. Variability among species in their responsiveness to synchrony in abiotic conditions could also play a role; for example, our dispersal matrix was a significant predictor of temperature synchrony (Supplementary material Appendix 4), a factor that was also a significant predictor of synchrony in *B. longirostris* and *D. lumholtzi* along with dispersal (results not shown). Pinel-Alloul et al. (1999) similarly found that spatial variation in temperature explained short-term plankton patchiness. Taxonomic differences in generation time, diel vertical migration patterns (Havel and Lampert 2006), sensitivity to wind patterns in forming spatial aggregations (Tessier 1983, Blukacz et al. 2009, Seebens et al. 2013), or other factors could also play a role.

An alternative, though related, explanation of plankton synchrony in Kentucky Lake that our methods cannot distinguish from direct dispersal is trophically-mediated dispersal effects. For instance, flow-mediated dispersal of a zooplankton taxon may directly synchronize that taxon, or, alternatively, flow may synchronize phytoplankton biomass which in turn synchronizes the zooplankton taxon through trophic interactions, or vice versa. Dispersal of any species in the food web could, in principal, be the origin of synchrony, which then ramifies to other species through trophic interactions through either bottom up or top down forcing (Verreydt et al. 2012). It will be difficult to distinguish these alternatives – they should all produce similar spatial signatures of synchrony. Nevertheless, dispersal is the underlying synchronizing mechanism under all of these alternatives, albeit possibly acting indirectly (Verreydt et al. 2012). Synergies between dispersal and predation have previously been shown to affect synchrony in experimental studies in other contexts (Vasseur and Fox 2009, Vogwill et al. 2009). It would be interesting to explore these ideas further in a system for which data on dispersal of multiple trophic levels exists, or if predators and prey utilize dissimilar dispersal corridors (Powney et al. 2011), facilitating the discrimination of alternatives. These issues are discussed further in Supplementary material Appendix 5.

Synchrony typically declines with distance (Koenig 1999), but our results show declines do not occur over the spatial scale sampled by the KLMP in Kentucky Lake, a span of 30 km. Absence of typical distance–decay patterns may be a common feature of synchrony between sites within a single body of freshwater. Other studies of synchrony in one freshwater body have also documented absent or minimal declines across greater distances than ours (> 100 km), as well as generally high levels of spatial synchrony for a variety of taxa (Grenouillet et al. 2001, Michaletz and Siepker 2013, Seebens et al. 2013, Lodi et al. 2014). In contrast, synchrony is typically weaker between pairs of water bodies (Cattanéo et al. 2003, Rusak et al. 2008, Michaletz and Siepker 2013), and does decline with distance for some taxa (Rogers and Schindler 2008), though such tests are absent from other between-water body comparisons (Cattanéo et al. 2003, Rusak et al. 2008). Greater environmental and physical variation and much reduced dispersal between water bodies compared to within them seem likely to be the main reasons for lower average levels of synchrony between water bodies. Movement of plankton within a water body can be substantial (Michels et al. 2001b), probably much more than dispersal via space or time (through egg banks) between water bodies (Havel and Shurin 2004).

Differentiating the mechanisms of spatial synchrony has historically proved challenging, due in part to the complexities of quantifying the variables necessary for comparative tests, and also due to the statistical similarity of each mechanism's effects using the most common statistical approaches, declines of synchrony with distance (Koenig 1999, Abbott 2007). Our approach is one solution to the problem: we move beyond declines of synchrony with distance to using detailed geographic patterns to facilitate tests of competing hypotheses concerning mechanisms of spatial synchrony (Haynes et al. 2013, Gouveia et al. 2016). We used this strategy to discover that hypothesized spatial heterogeneity in dispersal explained the spatial heterogeneity of synchrony for phytoplankton and zooplankton, even after controlling for numerous alternative mechanisms. Dispersal was therefore a likely mechanism of synchrony in our system. Further investigations of spatial synchrony that incorporate a similar approach to ours in other field systems may also provide an effective means of evaluating the importance of dispersal more generally as a mechanism of synchrony.

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Supplementary material (available online as Appendix oik-04705 at <www.oikosjournal.org/appendix/oik-04705>). Appendix 1–5.