

# ECOGRAPHY

## Research article

### Codistribution as an indicator of whole metacommunity response to environmental change

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The landscape scale response of ecological communities to environmental drivers can be challenging to efficiently summarise and differentiate from expected background turnover through time. Metacommunity structure can be encapsulated by fitting joint species distribution models (JSDMs) and partitioning the variance explained into environmental, spatial and species-codistribution components. Here we identify how these components respond through time with directed environmental change and propose these changes in metacommunity structure as an indicator of sustained directional pressure. Through simulations, we identify how declines in the variation explained by species codistribution could diagnose ecological disintegration, while increases in the explanatory power of environmental and spatial predictors may indicate losses in peripheral areas and dispersal limitations. We then test these results in two well-studied systems. Butterflies are known to be strongly responding to climate change, and we show that over 21 years the codistribution component declines for butterfly communities in southern England. By contrast, birds in the same region are thought to be responding less strongly to climatic pressure and, despite high occupancy turnover, do not show clear changes in metacommunity structure as measured by this approach. Our results suggest that these approaches could have a high potential to summarise and compare the impacts of external drivers on whole communities.

Keywords: butterfly, climate change, codistribution, joint species distribution model (JSDM), metacommunity, species associations, variance partitioning

#### Introduction

How can we tell when external environmental drivers, such as climate change, are impacting communities? Without further contextualisation, simply observing a change at a single location is insufficient, as communities are commonly subject to a considerable ongoing compositional turnover (Dornelas et al. 2013, 2014, Magurran et al. 2019) that is not necessarily associated with observable environmental change (Baselga et al. 2015). Community dynamics can be driven by ongoing



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environmental stochasticity as well as entirely endogenous processes (O'Sullivan et al. 2021) or ecological drift (Gilbert and Levine 2017). Separating 'background' community variability from that caused by directed environmental change is a considerable challenge, especially given that community reorganisation is not an instant process (Magurran et al. 2019). Metacommunity analyses, which examine multi-species responses across multiple sites, offer the potential to identify consistencies that could indicate the impact of an external driver.

Summarising high-dimensional (multi-species, multi-site and multi-time) data into informative metrics is a long-standing, but crucial, challenge for understanding and addressing large-scale ecosystem change. Clearly, answers to this question will depend on the type of data available. Where trait data related to environmental preference are available, community trait shifts can give clear indications of a directional driver (Wieczynski et al. 2019, Engelhardt et al. 2022). However, such data are not always available, and the overall picture that emerges may be complex as species within a community may respond differently (Antão et al. 2022). It is not always clear what the most relevant traits or environmental factors are, or if there even is a single key driving variable rather than a suite of stressors.

Recent developments in metacommunity ecology (Leibold and Chase 2018) provide a scaffold to increase the spatial and temporal scale of classic community ecology to address these problems. Much research effort has been directed towards identifying and comparing the mechanisms that structure different metacommunities (Ovaskainen et al. 2019, Blanchard et al. 2020, Jabot et al. 2020). However, distinguishing even the relative contributions of different mechanisms from observations of metacommunities remains a considerable challenge and likely requires substantial temporal replication (Guzman et al. 2022). Joint species distribution models (JSDMs) (Warton et al. 2015, Ovaskainen et al. 2016, 2017) are multi-variate regression models that provide a powerful tool to examine the complex patterns in spatially replicated community data. When JSDMs were initially proposed, the residual associations between species were identified as representing hypotheses for interactions between species. However, recent theoretical (Dormann et al. 2018, Zurell et al. 2018, Blanchet et al. 2020, Poggiato et al. 2021, Calcagno et al. 2022) and empirical (Barner et al. 2018, Freilich et al. 2018, Brazeau and Schamp 2019, Thurman et al. 2019) research has emphasized the poor correspondence with direct species interactions and the breadth of other factors that could determine the observed correlations in species responses. In particular, co-occurrences of species can be attributable not to direct species interactions, but rather to additional unmeasured environmental variables that are likely to obscure any underlying signal of species interactions (Blanchet et al. 2020).

Here we propose that rather than being a shortcoming of JSDMs, this synthesis of underlying mechanisms can be seen as an opportunity to detect the impact of unmeasured (or unmeasurable) environmental change on whole

communities. Interspecific associations are increasingly recognised as an important component of biodiversity monitoring, and can be quantified in a very large number of ways (Keil et al. 2021). Inter-regional comparisons have linked anthropogenic disturbance to disruption of cooccurrence patterns in stream invertebrates (Larsen and Ormerod 2014) and mammals (Gorczynski et al. 2022). The JSDM-based metacommunity variance partitioning approach described by Leibold et al. (2022) summarises the structure of a metacommunity by dividing the total explanatory power of the JSDM three ways: into that provided by spatial association, known environmental determinants and codistribution between species. We find in simulated mechanistic metacommunity models that directed environmental change is frequently characterised by a reduction in the variance explained by the codistribution component, and increases in the spatial and environmental components. We then apply the method to two well-studied empirical systems. Like other JSDM tools, the overall approach is flexible enough to incorporate various sources of data, but importantly is capable of identifying signals of directed change without either trait data or direct knowledge of any putative driving variable.

## Material and methods

The approach relies on fitting and comparing a series of JSDMs that predict the distribution of a community of species across a set of sites using environmental and spatial predictor variables. There are now numerous tools to fit JSDMs (reviewed by Wilkinson et al. 2019), although most differ principally in their approach to optimisation and, in principle, our approach is largely agnostic with respect to the optimisation approach used. Here we use species-by-site presence-absence data, since they are considerably more widely available, but we note that JSDMs can also fit abundance data, and this approach is likely applicable in that case too. However, statistical tools to assess the goodness of fit of count or abundance data are less well developed than for binary responses, and further research may be necessary to identify possible unwanted biases in the variance partitioning. The method requires community data for a set of sites from at least two time points that are to be compared. We exclude species that fall below or above site occupancy thresholds in any year to maintain sufficient variance in occupancy to represent an informative statistical target – ubiquitous or species with very low occupancy carry little information and so have little underlying data variance to meaningfully explain and partition. We determine these thresholds separately for each application.

### JSDM fitting, variance partitioning and identifying shifts

We fit our JSDMs with a probit link function using the 'HMSC' R package (ver. 2.2) ([www.r-project.org](http://www.r-project.org), Blanchet et al. 2019) that fits the models via Markov Chain

Monte Carlo (MCMC) optimisation. Latent variables identify residual codistribution of species as a separate element of the model (Warton et al. 2015, Ovaskainen et al. 2017) (Fig. 1a), simplifying the full cooccurrence matrix into a greatly reduced number of variables. The number of latent variables used is determined as part of the fitting process. We assume that the location of the sites is known and here represent spatial autocorrelation by the Moran eigenvector map (MEM) approach (Dray et al. 2012), decomposing the spatial coordinates using the *dbmem* function in the 'adespatial' R package (www.r-project.org, Dray et al. 2022) and selecting the first 10 components to use as spatial predictor variables. This approach has been found to be amongst the best at partitioning environmental and spatial drivers (Viana et al. 2022) and this number of components gave us sufficient spatial resolution and comparable numbers of spatial and environmental variables in our empirical examples. We assume that some environmental variables thought to be relevant to the distribution of the species in the metacommunity are known for each site and are taken to be fixed through time.

The variance partitioning is carried out following Leibold et al. (2022) by sequentially fitting seven models that make use of each possible combination of the spatial autocorrelation variables (Sp), measured environmental variables (En) and latent variables capturing species codistribution (Co), i.e. Sp, En, Co, Sp&En, Sp&Co, En&Co and 'All'. For each model the total variance explained (i.e. including whichever random and fixed factors are included in the model in question) for each species is described using the conditional

$R^2_{GLMM}$  method (Nakagawa and Schielzeth 2013). Grouping some terms, this is calculated for each species separately as:

$$R^2_{GLMM(con)} = \frac{\sigma^2_{model}}{\sigma^2_{model} + \sigma^2_{error} + \sigma^2_{distr}}.$$

where  $\sigma^2_{model} = (\hat{Y} - \bar{Y})^2 / (n - 1)$ ,  $\hat{Y}$  is the model prediction on the link scale (i.e. before transformation back from the unbounded scale to between 0 and 1),  $\bar{Y}$  is the mean value on the linked scale,  $n$  is the number of sites,  $\sigma^2_{error}$  is the remaining variance unexplained by the model and  $\sigma^2_{distr}$  is the distribution specific variance – in the case of probit link functions this is 1 (Nakagawa and Schielzeth 2013). To account for the way the models differ in the number of parameters they include, an adjusted- $R^2$  metric is used that can handle latent variables (Gelman and Pardoe 2006):

$$R^2_{adjust} = 1 - \frac{(1 - R^2_{GLMM(con)})(n - 3)}{n - p - 2},$$

where  $p$  is the total number of fixed effects and latent variables estimated.

The fractional variance explained by each model component and interaction is determined using a Type III variance partitioning approach (Peres-Neto et al. 2006), working backwards from the most complex model to identify single effects and overlap terms (Fig. 1b). Then, to more efficiently

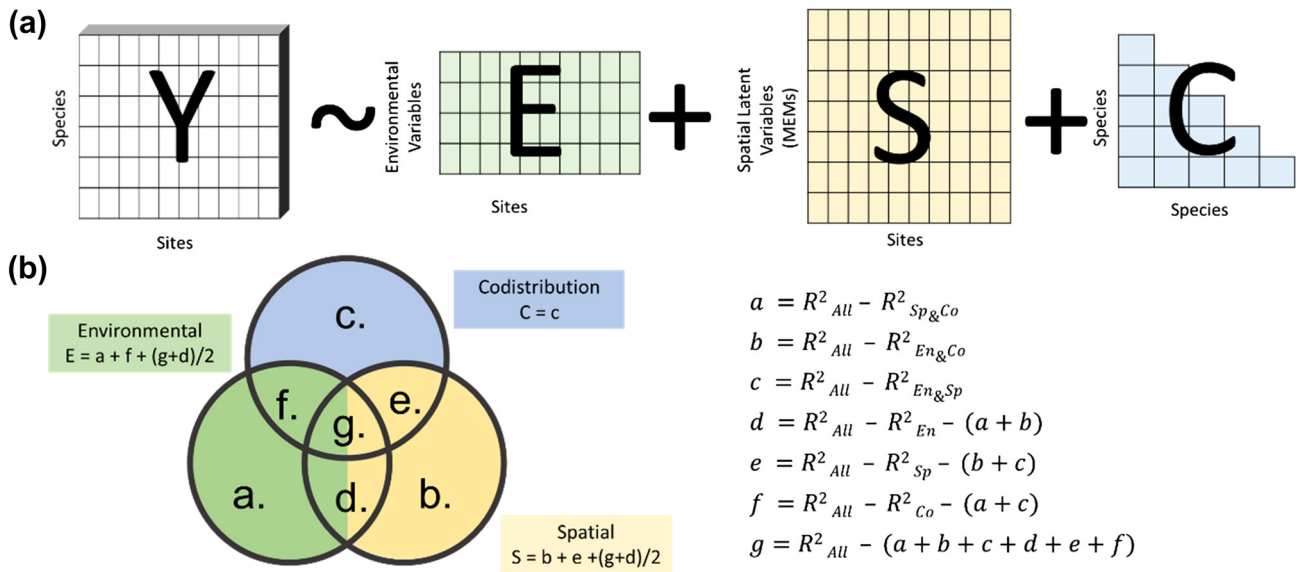


Figure 1. (a) General illustration of inputs to our joint species distribution model (JSDM). For each time slice we obtain a *species*  $\times$  *site* matrix (**Y**) that we wish to predict using some combination of environmental, spatial and codistribution information. Note that codistribution between species is illustrated here by a correlation matrix between species but, to reduce the number of parameters, we use a latent variable approach to summarise the correlation matrix into several latent factors for which each species has a factor loading (Ovaskainen et al. 2017). (b) Having fit seven JSDMs using each possible combination of the three sets of information (spatial predictor variables Sp, environmental predictor variables En, species correlations Co, Sp&En, Sp&Co, En&Co and All), differences in the  $R^2$  of each model (calculated as per details in the main text following Leibold et al. 2022) are used to partition the overall variance explained into sub-components (single effects and interaction terms, represented by sections of the Venn diagram). These are then summed into the three components of interest.

summarise these seven quantities, we again follow the approach of Leibold et al. and group the sub-partitions of the total variance explained into three partitions of interest. The sub-partitions overlapping with codistribution (Venn segments 'f', 'g' and 'e' in Fig. 1b) are assigned to the spatial and environmental partitions, respectively, because the flexible latent variables are likely to efficiently capture residual variance in the combined models. The variance explained by the combination of environmental and spatial predictors (Venn segments 'g' and 'd') is split 50:50 between them. To move from species-level partitions to a whole-community value we average across all the species (equally weighted). This variance partitioning process is repeated for each time slice, fitting each model independently. We then examine the changes through time in the variance explained by each of the three components.

## Simulation

To examine how the partitioning of the explained variation changes under known and controlled conditions, we used a mechanistic metacommunity model within the simple discrete-time Lotka–Volterra framework described in Box 1. These metacommunities are imagined to represent a set of sites within a wider landscape, and so are subject to both local dispersal amongst sites and some ongoing dispersal from 'outside' the observed system. We built a large set of distinct

metacommunities, following a Latin-square design spanning six levels each of four parameters determining interspecific competition ( $\alpha$ , 0.2:1.1), growth rates ( $\gamma$ , 5:50), dispersal rate ( $\delta$ ,  $10^{-5}$ : $10^{-2}$ ) and environmental stochasticity ( $\sigma$ ,  $10^{-3}$ : $10^{-1}$ ), with two repeats at each combination ( $6^4 \times 2 = 2592$  communities in total). Figure 2 shows the partitioning of an example simulated community, but where we conduct the variance partitioning for each time slice from  $t=951$  to  $t=1000$  illustrates the extent of underlying variation.

For the main simulation, abundance data from just before the onset of the environmental change ( $t=975$ , 'before') and from 25 years after the onset of directional change ( $t=1000$ , 'during') from the central 100 sites of the arena were extracted and converted to presence/absence using a threshold biomass of 0.1. Species that had a total occupancy  $\geq 5$  and  $\leq 95$  (out of 100 sites) in both time slices were retained. For all the 'before' and 'during' time slices, we fit separate JSDBMs to conduct the variance partitioning as described above (total MCMC iterations 20 000, burn in=10 000, thinning factor=10, which trials suggested was more than sufficient for convergence). We fit the models using the initial values of the environmental variables  $E_1$ ,  $E_2$  and their quadratic transformations as environmental predictors. We do not include observations of changes to the environmental variables. The simple nature of our model would in any case make linear offsets uninformative. Observation error is known to be able to disrupt the accurate fitting of JSDBMs (Beissinger et al.

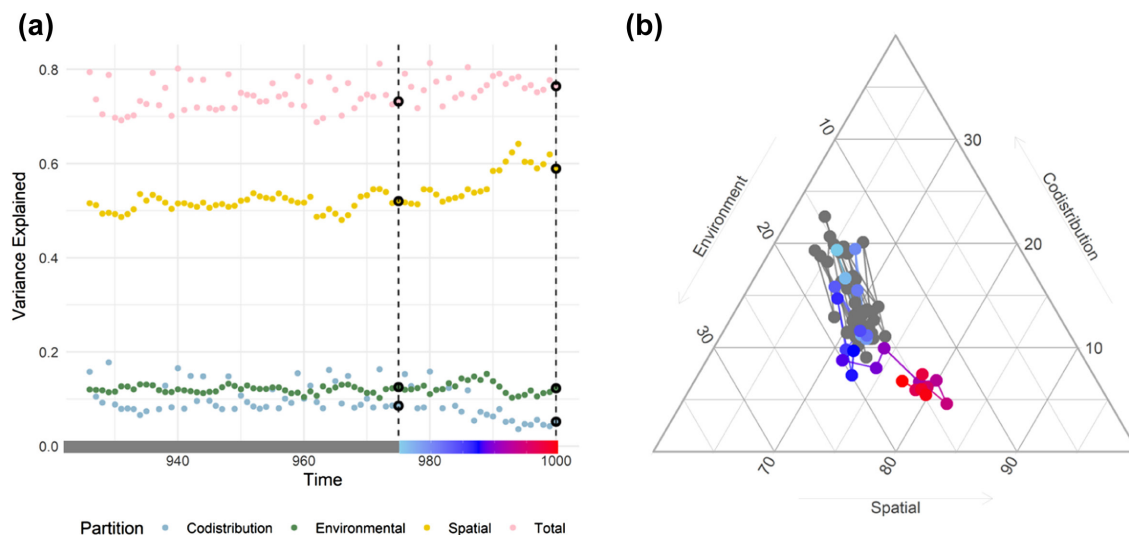


Figure 2. Example of how simulated metacommunity structure changes before and after onset of directional environmental change (at  $t=975$ ), as measured by the variance explained by the three partitions. (a) Values of the three partitions of the total variance explained by joint species distribution models (JSDBMs) fit to each time point. Ongoing fluctuations before the onset of the driver in measured metacommunity structure are attributable to a mixture of background environmental stochasticity, intrinsic dynamics of the system (driven by competition and incoming dispersal) and a small amount of model fitting error. Vertical lines show the two sampling points used in the full simulations ('before' and 'during'). (b) The same data, depicted on a ternary plot, since the total variance explained (pink) shows no trend. Each point is the state of the community at a particular time slice. Grey points show 50 time points before the introduction of directed environmental change. Coloured points depict the amount of environmental change (panel a). In this example, the community structure responds to the onset of the change, after a brief delay, to reduce the codistribution contribution and increase the spatial contribution (i.e. moving to towards bottom right of the ternary plot). Ternary plot made using 'ggtern' R package ([www.r-project.org](http://www.r-project.org), Hamilton and Ferry 2018). Simulation model parameters used:  $\alpha = 0.31$ ,  $\gamma = 10.4$ ,  $\delta = 0.0028$  and  $\sigma = 0.01$ .



2016). We examine the potential for this to be a problem in the Supporting information, by showing the overall robustness of the approach to the random introduction of false negatives to the dataset.

### UK butterfly transect test

To examine if the pattern identified in the simulations is also discernible in real data, we used data from the United Kingdom Butterfly Monitoring Scheme (UKBMS). These highly curated data consist of 1–2 km long transects regularly

surveyed by trained volunteers across the UK. Because UK Lepidoptera are known to be undergoing climate-change-driven range shifts, albeit influenced by landscape structure (Parmesan et al. 1999, Roy et al. 2001, Warren et al. 2001, Mair et al. 2012, Oliver et al. 2017), this dataset provides a ‘known target’. While the whole dataset covers surveys from 1976 to the present, we focus on data from 2000–2020 because in this period a large number of sites were continuously monitored.

We selected English transect sites which had been walked at least five times within at least 18 of the 21 years in our study

### BOX 1. Mechanistic metacommunity simulator

All communities were built on a square grid of 196 sites, each connected to their immediate neighbours (Supporting information). Boundaries were connected as if on a torus, so each site had four neighbours. The biomass of species  $i$  at site  $z$  at time  $t + 1$  is given by:

$$B_{i,z,t+1} = B_{i,z,t} + \theta B_{i,z,t} \left( \gamma R_{i,z,t} - \sum_j C_{ij} B_{j,z,t} \right)$$

where  $R_{i,z,t}$  is the local growth rate,  $C_{ij}$  is a competition matrix including inter and intraspecific competition, and  $\theta$  is a timescale parameter, set to 0.1.  $\gamma$  is a simulation control parameter that controls the rate of intrinsic growth. The model is advanced in blocks of 10 time steps, which we refer to as a ‘year’.

Each site was assigned two explicit environmental variables ( $E_1$ ,  $E_2$ ).  $E_1$  represents a variable that will change through time, and could be considered ‘temperature’. It increases from left to right of the arena. Each year it is subject to additive stochastic noise drawn from a Gaussian distribution with mean 0 and standard deviation  $\sigma$ .  $E_2$  represents an environmental variable that stays constant through time, for example the underlying geology. It increases up the arena (Supporting information). The growth rate of each species  $R_{i,z,t}$  is calculated using a cosine-based environmental performance function:

$$R_{i,z,t} = R_{i,z}^* \times \sqrt{\cos(\pi(E_{1,t} - \psi_{1,i}))^2 \times \cos(\pi(E_2 - \psi_{2,i}))^2}$$

where  $\psi_{1,i}$  and  $\psi_{2,i}$  are species specific optima for each environmental variable. Additional idiosyncratic species-specific site preferences are represented by also generating and incorporating a random species  $\times$  site matrix  $R^*$ . While complex, this function was chosen as it introduces moderate synergistic dependence on multiple environmental variables, it is always positive, its upper limit is controlled, and it approximately maintains the range size of each species within the full arena as  $E_1$  shifts.

Species are drawn from a global pool of 50 species each with randomly generated  $\psi_{1,i}$  and  $\psi_{2,i}$  values drawn from independent uniform distributions (0:1) and  $R_{i,z}^*$  with uncorrelated entries drawn from a uniform distribution ranging from 0.2 : 1. The competition matrix  $C$  between these species is relatively sparse and semi-structured to ensure that each species affects and is affected by at least one species. Overall results were almost identical using completely unstructured interactions. The species were ordered randomly, without relation to the environmental preferences, and each species  $i$  exerts competitive pressure on the next species in the sequence (i.e. the lower-subdiagonal, Supporting information). Additionally, random competitive effects are also introduced to  $C$ , with probability 0.01. All interspecific interactions have the same coefficient,  $\alpha$ . The intraspecific (diagonal) elements are all set to 0.1.

Dispersal between sites and into the system is added at the start of every year. Local dispersal incoming into each site from the neighbouring sites  $n$  is calculated from  $I_{i,z,t} = \delta \sum_n B_{i,n,t}$ . In addition, dispersal into the system from the global species pool is included. One species randomly selected from the global pool is each introduced to each site with probability 0.1 at density 0.0001.

Communities are initiated by starting a randomly selected half of the species in the global pool at a density of 1, each at a different randomly selected site. The simulation is run for a burn-in period of 975 years, during which the total species richness and range size distribution of the community reaches a steady state while the metacommunity continues to show ongoing turnover at local scales.

Directional environmental change is introduced by increasing  $E_1$  across the whole arena by 0.01 each year, for 25 model years. This corresponds to a displacement in the environmental envelope of each species equal to about half of the total range (see example below, full details in the Supporting information).

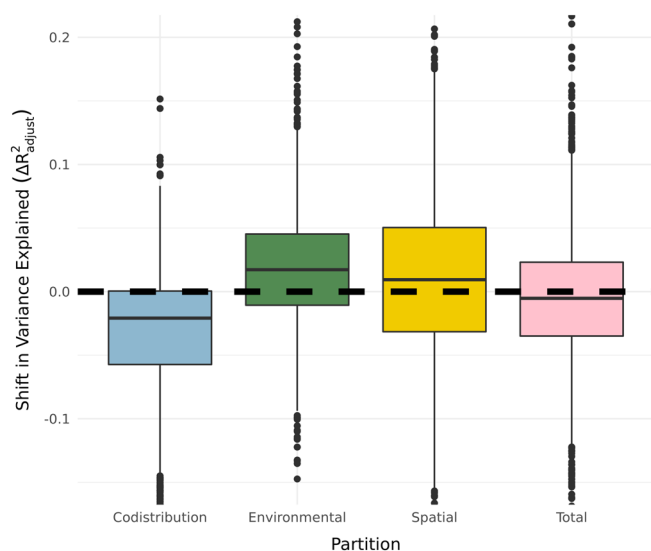
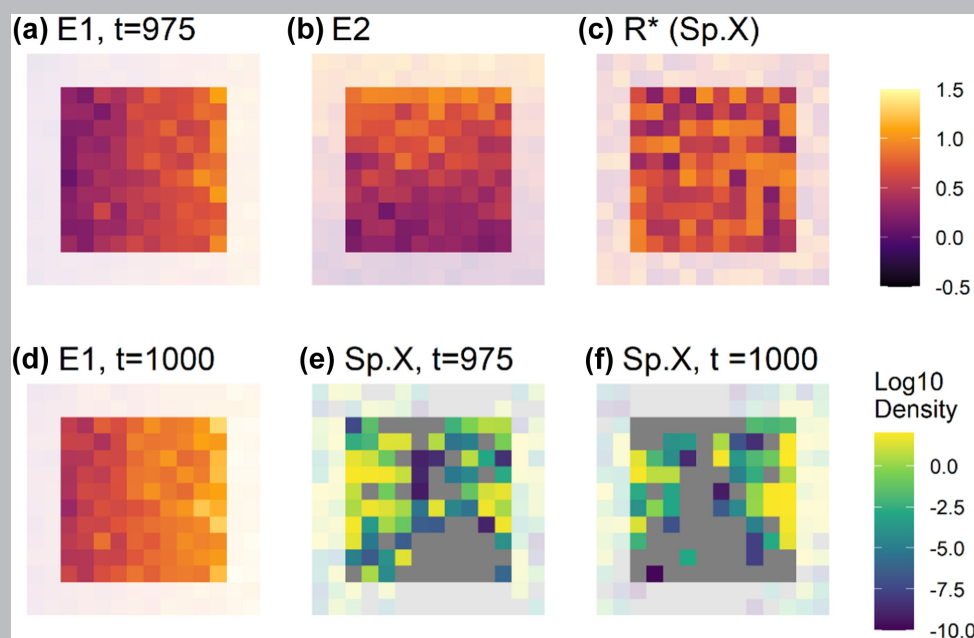


Figure 3. Distribution of shifts in the variance explained by each of the three components between the 'before' and 'during' environmental change time slices, across the full set of 2592 simulated communities spanning a wide range of parameters. Boxplots hinges show 25 and 75th percentiles, whiskers extend  $1.5 \times$  inter-quartile range. Note that a few outliers have been clipped from the figure to maintain emphasis on the bulk of the distribution (largest observed shift was in cocodistribution,  $-0.334$ ). All mean shifts were significantly different to zero (two-sided t-tests,  $p < 10^{-6}$  and  $n = 2592$ ).

period, and were south of  $53.5^\circ$  latitude and east of  $-3.5^\circ$  longitude (thus excluding outlying peripheral sites in the west and north of England with distinct habitat types, Supporting information). We grouped individual transect walks within each year, to determine if each species was observed at least once in that year. We excluded moths (which are not consistently recorded at all sites), migratory species *Colias croceus* and *Vanessa cardui*, and species with mean occupancies  $< 2\%$  or  $> 98\%$ . Species' status during missing surveys (mean 1.57 years were missing per focal transect) were inferred based on whether each species was present in both the immediately preceding and following surveys (inferred to be present in the gap), absent in both preceding and following (inferred to be absent). If the species was present at the site in just one of the preceding or following surveys, it was randomly assigned to be present with probability equal to its occurrence frequency at that site across the whole time period. This filtering process left 42 species and 97 sites. Overall occupancy through time was relatively constant (Supporting information).

For each transect site, environmental information was gathered by cross-referencing the associated UK national grid cell (from the middle of the transect) with national databases. Habitat values of each site were inferred from a 2000 UK land cover map raster at 1 km resolution (Fuller et al. 2002). Although land cover changes are possible over the examined period, most sample sites are in relatively protected areas, and we do not expect widespread changes over the period. We generated four land cover variables for each site from summing key percentage land cover categories: Woodland ('Coniferous

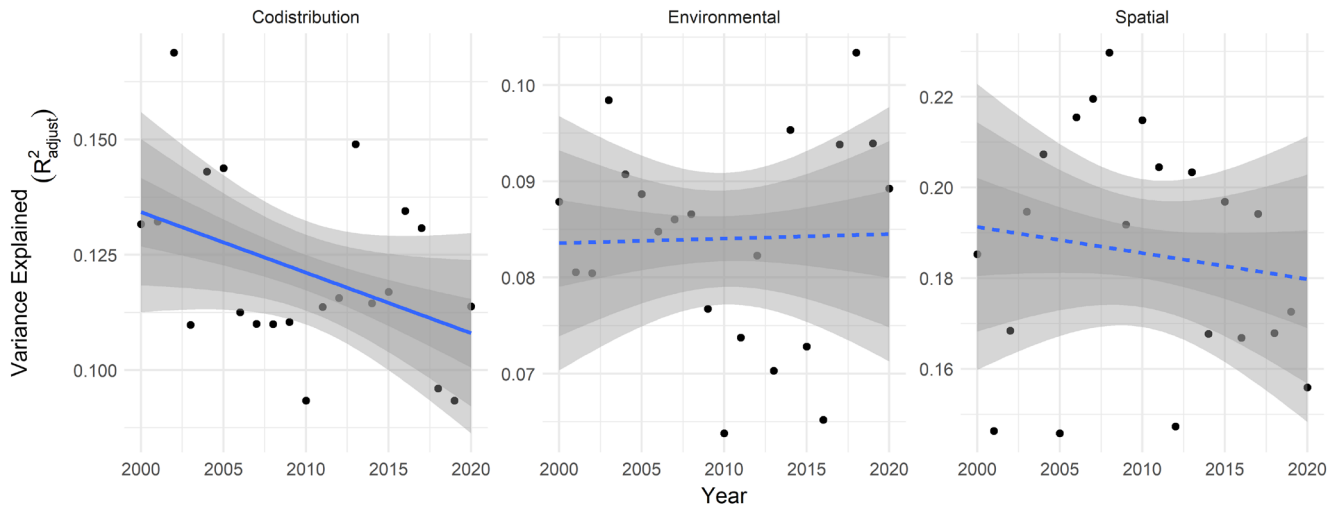


Figure 4. Trend in metacommunity structure as explained by each of the three components of the United Kingdom butterfly monitoring scheme (UKBMS) butterfly dataset through time. Lines show linear models. The variance explained by the codistribution component shows some evidence for a negative trend ( $-0.0013 \text{ year}^{-1}$ ,  $p = 0.0575$ ), while other partitions showed minimal evidence of a linear trend (Environmental:  $p = 0.906$ , Spatial:  $p = 0.548$ ). Shaded regions show 66, 95 and 99% confidence intervals for the slopes.

Woodland', + 'Broadleaved woodland'), Farming ('Arable horticulture' + 'Arable cereals' + 'Improved grassland' + 'Arable non-rotational'), Urban ('Continuous urban' + 'Suburban/rural developed') and 'Calcareous Grassland' on its own. The Woodland, Urban and Calcareous Grassland variables were  $\log(x+1)$  transformed to better normalise their distribution. Calcareous grasslands are a key habitat type for European butterflies (van Swaay 2002), but within the land cover map we used this is a broad habitat type that includes other high-pH grassland types. We therefore added a binary 'chalk' variable for each site based on the distribution of 'high' and 'high(variable)' in the carbonate content field of the British Geological Survey soil parent material 1 km dataset (Lawley 2012). As a baseline temperature variable, the mean average temperature of each site over the period 1961–1990 was inferred from a 5 km climate grid (HadUK-Grid, Hollis et al. 2019). The longitude and latitude coordinates of the selected sites were used to infer the first 10 MEM components.

We conducted the tripartite variance partitioning separately for each of the 21 years in our sample period. For each submodel we ran very long MCMC chains (total sampling 100 000, burn-in = 50 000, thinning = 50). To confirm this was sufficient for convergence, we ran two MCMC chains of the full model and checked all values of the Gelman–Rubin diagnostic  $\hat{R}$  (Gelman and Rubin 1992) via the 'coda' R package (www.r-project.org, Plummer et al. 2006). To assess

the statistical significance of trends through time in the variance explained by each component we fit separate linear models through each of the components against year.

### UK breeding bird atlas test

As a second test case, we used atlas data of UK breeding birds from the extensive 1970 and 2010 breeding bird surveys (Gillings et al. 2019). This is a highly curated citizen science dataset detailing the presence of all breeding birds in each  $10 \times 10 \text{ km}^2$  of the UK national grid. Survey methods were calibrated to allow comparability between the 1970 and 2010 surveys. To exclude coastal-specialist species and focus on inland bird communities we used data from 348 grid cells from a rectangle of central England without coastline ( $51^\circ$  to  $54.3^\circ$  latitude,  $-2.3^\circ$  to  $-0.9^\circ$  longitude, Supporting information). We excluded non-native species (i.e. not category A or C2 in the British list (McInerney et al. 2018)) and those that occurred in  $\leq 5$  focal cells, or were recorded as absent in  $\leq 5$  focal cells, in either year. This filtering process left 80 species. The total number of observed records in our dataset in each year was remarkably consistent (1970 = 12 950, 2010 = 12 798), but there was high turnover in site occupancy over this period, both within and between species (Gillings et al. 2019, Wayman et al. 2022). The breeding bird survey categorises the quality of observations into 'confirmed', 'probable' or

Table 1. Comparison of the components of the variance partitioning of joint species distribution models (JSDMs) fit to the breeding bird atlas datasets from central England between the 1970 and 2010 surveys.

Dataset	Year	Total occupancy	Variance explained			
			Environmental	Spatial	Codistribution	Total
All records	1970	46.5%	0.333	0.131	0.088	0.552
	2010	46.0%	0.352	0.118	0.087	0.558
Excluding 'possible' records	1970	43.7%	0.361	0.108	0.097	0.566
	2010	40.3%	0.330	0.110	0.095	0.536

‘possible’. We repeated our analysis, excluding the ‘possible’ observations (which, with the filtering procedure described above, reduced the number of species to 75).

We determined environmental variables for each  $10 \times 10$  km grid cell from the 1990 (i.e. intermediate between the sample years) 1 km grid UK landcover map (Rowland 2020), calculating total percentage cover of 11 habitat variables using a mixture of specific target classes and some aggregate classes. These were: *Broadleaved Woodland*; *Coniferous Woodland*; *Arable and Horticulture*; *Improved Grassland*, *Neutral Grassland*; *Calcareous Grassland*; *Acid Grassland*; *Fen, Marsh and Swamp*; *Freshwater*; *Mountain, Heath and Bog*; *Urban and Suburban*. Elevation and climate variables correlated strongly with these habitats, and so these were not included. The longitude and latitude coordinates of the selected sites were used to infer the first ten MEM components. Model fitting (total sampling: 50 000, burn in: 30 000, thinning: 20), convergence checking and variance partitioning was conducted as for the UKBMS data, but with only two years we did not test for the significance of trends through time.

## Results

Across the full set of simulations comparing metacommunity structure ‘before’ and ‘during’ the environmental change, there was a clear tendency for a reduction in the variance explained by the codistribution partition, and a moderate trend for increases in the variance explained by the spatial and environmental partitions (Fig. 3, Supporting information). The overall variance explained by the model showed minimal trend. Overall occupancy of the focal species  $\times$  site matrix remained essentially constant (‘Before’: mean occupancy = 61.9%, ‘During’ mean occupancy = 62.2%), despite considerable turnover (Jaccard dissimilarity of site occupancy vectors of each species between ‘before’ and ‘during’ samples mean = 0.306, SD = 0.099).

The underlying dynamics (as determined by the four simulation control parameters) impacted the starting structure of the metacommunities (Supporting information). For example, higher levels of interspecific competition reduced the average occupancy rates of the assembled communities, as well as increasing the variation in range size between species. Hence, higher competition also led to greater explanatory power for spatial structuring, while high levels of environmental stochasticity reduced the initial codistribution component.

However, simulation model parameters had relatively little influence on the changes in variance explained by each partition between the time points (Supporting information). The bulk of codistribution shifts were negative in all cases except for very high stochastic environmental variability where there was no consistent shift in explanatory power of any of the partitions. The variance explained by the environmental partition tended to be larger after climate change across all parameter combinations. Changes in the explanatory power of the spatial partition were the most

parameter sensitive, with the most consistent increases seen in parameterisations where the core growth rate was higher and competition was relatively weak. The introduction of false absences at high levels (e.g. 20%) led to a small reduction in the extent of the identified shifts in metacommunity structure (Supporting information) but not the overall pattern.

In the butterfly dataset, there was some support for a reduction in the variation explained by the codistribution partition (Fig. 4,  $-0.0013 \text{ year}^{-1}$ ,  $p = 0.0575$ ). Minor modifications in data filtering and predictor transformation can move the final p-value across the classic 0.05 critical threshold, but maintain the same trend. The environmental and spatial partitions showed no identifiable trend (Fig. 4). See Supporting information for species level variance partitions, fitted environmental associations and species associations.

The breeding bird dataset did not show large changes in overall metacommunity structure (Table 1), despite considerable occupancy turnover (27% of species  $\times$  site occupancies changed between samples). Differences in codistribution structure were particularly small. Shifts in the environmental and spatial components were minimal and inconsistent depending on how the filtering was conducted.

## Discussion

Variance partitioning with JSDMs appears able to diagnose the impact of directed environmental change in complex communities. Despite continued challenges in the quest to identify underlying ecological processes from distribution snapshots (Gilbert and Bennett 2010), considerable progress is possible in other directions by seeking statistical features that indicate disruptions to the community structure. As we will argue, the observed shifts have meaningful ecological explanations in line with the expectations associated with the early stages of community disintegration, the generation of no-analogue communities and the role of dispersal limitations.

Our simulation model includes significant ongoing turnover, driven by continual immigration and competition, as well as underlying environmental stochasticity. This results in species average occupancy (and indeed the average site species richness) remaining approximately constant as the environmental change is introduced, in line with observations from many communities across the world (Dornelas et al. 2014, Pilotto et al. 2020). The observed shifts in the variance partitions can therefore be confidently identified as a signal of restructuring, not an artefact of loss of alpha-diversity.

Within the controlled virtual world of our models, the consistent pattern of metacommunity responses can be linked to ecological explanations. The reduction in the explanatory power of species codistribution can be interpreted as being indicative of ongoing disruption to communities that reduces the consistency of species co-occurrences. Communities take time to respond to their circumstances, and the ongoing disruption of continuous climate change



generates a persistent transient period in which previously established patterns can weaken. The greater reduction in the codistribution partition in simulation with lower dispersal rates (Supporting information) highlights the role of these lags. However, the detailed ecological mechanisms behind these effects are harder to pin down, because of the multitude of factors contributing to the original co-occurrence patterns (Blanchet et al. 2020). One pathway is that as species distributions respond to the change in climate at different rates across sites, colonisation and extirpation stochasticity reduces the consistency of communities across space. There is some evidence from mesocosms that consistent patterns of species sorting may be clearer in more established communities (Cadotte 2007). However, the extent to which this decline will be seen in a given real system will depend on the relative role of stochasticity over deterministic filters in determining the community structure. Disruption to cooccurrence patterns in more heavily modified regions has been identified in stream invertebrates (Larsen and Ormerod 2014) and there is also evidence that human action is introducing sustained changes to species associations during the Holocene (Lyons et al. 2016). We reiterate that there is no reason to interpret this as a tendency for weakening effective interspecific interactions – there is little basis to identify changes in codistribution with any potential direct changes in pairwise biotic interactions induced by environmental change (Tylianakis et al. 2008, Poisot et al. 2015).

One feature of our simulations is that the local diversity of each site is relatively consistent through time, in line with the results of many metanalyses examining local trends in species richness (Dornelas et al. 2014). However, where ecological stress causes widespread local extinctions of particular species, this can reduce the contribution of apparent randomness community structure (Chase 2007) and might be expected to lead to homogenisation and the possibility of an increase in the codistribution partition.

The frequent increase in the environmental partition can be heuristically explained in terms of species being forced out of marginal habitats with environmental values on the edges of their original limits. Linked to this, the increase in spatial association could be explained by a dispersal delay. As isolated, peripheral, populations far from the species core areas are lost, newly colonised areas are likely to be closer to the core areas that provide the greatest source of new dispersers. The net effect is an increase in the explanatory power of spatial association as spatial heterogeneity is reduced. This pattern of spatial homogenisation has been identified as a global response to current global change (McGill et al. 2015). The nature of our simulations (with a spatially structured environmental variable) can conflate the environmental and spatial aspects of this retrenchment processes.

We would not expect real examples of communities subject to environmental change to precisely follow the patterns identified in our simulations: different guilds have different inherent traits, are structured differently by interspecific competition, are under different environmental pressures and may be driven by fundamentally different dynamics. Nonetheless,

these simulation results provide an expectation against which empirical communities can be assessed and compared.

## Butterflies

The butterfly dataset showed some evidence for a decline in the explanatory power of the codistribution partition, indicating a weakening in the consistency of species co-occurrences in space. Butterflies show large annual variation, responding to annual weather fluctuations (Roy et al. 2001). As such, the ability to identify a trend through a relatively short time series is a notable achievement of the methods. The codistribution latent variables can capture correlated responses to unknown (or at least, unincluded) environmental variables (Blanchet et al. 2020). UK butterflies are considered to not directly interact with each other – they rarely share larval food resources, and possible apparent competition through shared parasitoids is not generally considered to be influential (Thomas et al. 2011, Thomas and Lewington 2014). The residual correlations between species occurrences that are captured by the codistribution latent variables can, in this case therefore, be attributed with some confidence to environmental determinants not included in our environmental variables. Inspection of the mean species association matrix (Supporting information) suggests a split into a small group of woodland species from species more often associated with grassland. The habitat requirements of UK butterflies are well known (Redhead et al. 2016). However key factors, particularly the availability of specific larval food plants, are only loosely captured by our coarse environmental variables. Higher-quality environmental predictors may be able to resolve stronger trends in both the residual codistribution and the environmental partitions. There was no hint of any change in the spatial association component through time. It is possible that dispersal limitation may not be relevant or detectable at the scale and resolution of our dataset. Butterfly dispersal capacity varies between species (Stevens et al. 2010), but in our dataset weaker dispersers, such as the Black Hairstreak *Satyrrium pruni* (Thomas et al. 1992), are mostly excluded because of their rarity.

## Birds

UK birds are undergoing considerable change, but across the highly heterogeneous community there would be less expectation that there are consistent driving variables compared to the butterfly dataset. To some extent, the bird data act as a ‘negative control’ for our method. Although the spatial scale is coarser than the butterfly dataset, the high degree of turnover suggests the resolution is sufficient to be able to capture distinct local populations. With just two time periods to compare, it is not possible to test statistically whether the changes in the spatial and environmental partitions represent a significant trend. However, we do find the apparent consistency, particularly in the codistribution component, worthy of note, especially within the context of the very high turnover rate. The fraction of observations listed as ‘possible’

confidence was higher in 2010, leading to a decline in total occupancy in the stricter dataset. A reduction in the spatial partition (as we observed in the larger dataset) would be in line with the findings of [Wayman et al. \(2022\)](#) who found a moderate increase in spatial heterogeneity through time using similar data. However, if real, this decline may have more complex drivers than those examined in our simulations. As strong dispersers, birds are likely to be less subject to the dispersal constraints that appear to drive the increase in the explanatory power of the spatial component in the simulations.

## Applicability and extensions

Expanding databases of biological monitoring data ([Record et al. 2021](#)) are opening up the potential to apply our approach more widely. Here we restricted ourselves to cases where we could fit each JSDM to the same sites and species through time, which excludes datasets where the coverage is large, but irregular. However, in principle this is not a necessity – if it can be reasonably assumed that the sampling of sites (and species) is consistent through time, more heterogeneous data sources can be used. Furthermore, while in both examples we used highly curated data sources where it is reasonable to assume that effect of observation errors is small, this may not be required. Although our simulations (Supporting information) suggest that the approach is quite robust to false absences, an important part of any deployment of the method will be assessing the impact of the imperfect detection of species ([Tobler et al. 2019](#)), which may be substantial and vary between both species and sites ([Beissinger et al. 2016](#)). Importantly, there is no particular need to have a pristine reference ‘before’ site with which to compare. While longer time series are informative, shifts in communities are expected to continue and accelerate, and ‘in progress’ shifts can also be detected.

A feature of the approach is that we use the same fixed set of environmental predictors for each dataset through time. This means that the raw information content of the environmental predictors is constant. We do not attempt to determine the specific drivers that may lie behind any disruption to communities. Moving from summary statistics describing how a community is changing to diagnosing a causal link to specific external environmental drivers poses considerable challenges ([Parmesan et al. 2013](#), [Oliver and Morecroft 2014](#)). Furthermore, any measure of a metacommunity must always be considered in terms of the spatial scale at which it is observed ([Leibold and Chase 2018](#)), although this scale dependence can be exploited to garner further ecological information ([Ovaskainen et al. 2016](#), [Elo et al. 2021](#), [König et al. 2021](#)). Examination of the responses of simulated models can clarify the expected direction of responses of metacommunities to different external pressures, and there remains significant scope for the exploration of different simulated models within this framework. Our measures of shifts in community structure are quantitative, but it is not yet clear how the magnitude of shifts in different systems (with

different scales and environmental variables) can be compared. On the optimistic side, there are plenty of ecological explanations for these shifts – these are tangible quantities that are changing. On the pessimistic side, for the very reason that there are plentiful ecological explanations, identifying exactly which mechanisms are key is likely to require considerable additional information.

One way to mitigate the risk of generating ‘just-so’ stories derived from a limited number of summary variables is to examine the species level responses. While we have focussed on the whole-metacommunity responses as a general signal, this is constituted of the averaged responses of individual taxa which can also give useful information (i.e. the internal structure of the metacommunity sensu [Leibold et al. \(2022\)](#)). Investigation of the species level responses can bring additional insight into the drivers of the overall change. Here, we took the simplest possible route to weight the explanatory power within species within the community, taking a grand mean. Future work could profitably investigate if different weighting procedures can identify informative trends. While our focus here is on a general method and the possibility of inferring signals without specific knowledge of the species concerned, an interesting avenue for future work would be to take advantage of the exceptional trait knowledge for both birds ([Tobias et al. 2022](#)) and butterflies ([Middleton-Welling et al. 2020](#)) to identify if drivers of species-level partitions can be identified.

## Conclusions

By providing a relatively simple summary of complex community-level spatial–temporal trends, variance partitioning of JSDMs has great potential to diagnose community responses. Residual species correlations identified through JSDMs have had a tumultuous recent history, with interpretations as interactions coming under particular considerable recent criticism ([Blanchet et al. 2020](#)). While measures of the extent of co-occurrence can be hard to interpret, *changes* in co-occurrence can identify community responses. There remain very considerable challenges around interpreting ‘mechanistically’ what these ultimately statistical measures signify, but with further validation in well-understood systems they have the potential to act as an early indicator of the road towards novel ecosystems ([Hobbs et al. 2009](#)) discernible through the noise of background turnover patterns.

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## Author contributions

**J. Christopher D. Terry:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (lead); Writing – original draft (equal); Writing – review and editing (lead). **William Langdon:** Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Axel G. Rossberg:** Funding acquisition (equal); Writing – review and editing (equal).

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## Data availability statement

Analysis code and data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.7729313>.

## Supporting information

The Supporting information associated with this article is available with the online version.

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