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Research article

The pace and drivers of community change vary over space and time – findings from a national biomonitoring programme

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Habitat heterogeneity and demographic processes create variability in the major taxonomic diversity trends: 1) biotic homogenization and 2) the emergence of novel community compositions. Nonetheless, little is known about how the imprints of environmental filtering and random demographic processes on community dissimilarity vary over 1) time or 2) space. Quantifying such variation is key to revealing temporal regime shifts, latitudinal trends, and site-level specificity in the drivers of community dissimilarity.

To characterise variation in drivers of community change, we introduce the concept of 'non-stationary community responses'. We then apply this concept to estimate temporal and spatial variability in the imprints of climate, land cover and random processes on spatial and temporal dissimilarity of community composition. As a model system, we use multidecadal monitoring data of bird (1147 monitoring sites; 49 years), butterfly (101 monitoring sites; 22 years), and moth (99 monitoring sites; 26 years) communities across a 1200-km latitudinal gradient in Finland.

Regarding spatial dissimilarity, environmental filtering had a larger imprint than what random processes had. For butterflies and moths, environmental filtering shifted from being primarily associated with land cover to being primarily associated with climate indicating a likely regime shift along with warming climate. Regarding temporal dissimilarity of bird and butterfly communities, the imprints of environmental filtering and random processes varied between monitoring sites. A conventional stationary model was unable to track such site-specific processes. The imprints did not change linearly along a latitudinal gradient.

Our results demonstrate that accounting for non-stationarity in community dynamics is needed to pinpoint temporal shifts and spatial variability in the drivers of community

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change. Should we assume that community change is driven by the same primary forces at all times and everywhere, then we will fail to detect the real local and contemporary drivers of change, and risk applying the wrong corrective measures.

Keywords: assembly processes, Bayesian inference, beta-diversity, climate change, community change, land cover

Introduction

Across the world, communities (here: the set of species recorded at a given locality during a given year) are rapidly changing due to intense land-use practices, shifting climate, invasive species and increasing direct exploitation (Newbold et al. 2015, Jaureguiberry et al. 2022). As key outcomes of community change, we may expect biotic homogenization, i.e. a decrease in the spatial variability of communities' composition (Ekroos et al. 2010, Magurran et al. 2015, Newbold et al. 2018) and the emergence of novel local community compositions, i.e. an increase in community dissimilarity over time (Ordonez et al. 2016, Ammar et al. 2021).

Biotic homogenization and novel communities have indeed been detected in large-scale analyses. Nonetheless, strong variability across time appears a general theme in biotic homogenization (Blowes et al. 2019, Daru et al. 2021, Blowes et al. 2022), and spatial variability a general pattern in the emergence of novel communities (Daskalova et al. 2020, Ammar et al. 2021). To understand such context-dependency in biodiversity trajectories in space (homogenization) and time (novel communities), we should resolve whether shifts in community composition are consistently driven by the same forces when multiple communities are compared over space in the same year, or the same community is followed over multiple years (Jarzyna et al. 2014). We argue that tracking the variability of the drivers of community dissimilarity over time and space is a key prerequisite for understanding the sensitivity of ecosystems to global change from national to continental scales.

Earlier studies have detected variation in the drivers of community dissimilarity. For spatial dissimilarity, the effects of individual drivers have been found to vary between time periods (Stegen et al. 2013, Datry et al. 2015, Rolls et al. 2023), and for temporal dissimilarity, effects have been reported to differ between habitat patches (Stegen et al. 2013, Jarzyna et al. 2014, Datry et al. 2015, Rolls et al. 2023). Non-stationary responses across time or space can result from non-equilibrium populations dynamics (Nuvoloni et al. 2016), species tracking seasonally suitable habitats (Datry et al. 2015), stochastic sampling effects (Stegen et al. 2013), demographic stochasticity (Engen et al. 2017) or environmental stochasticity (Rolls et al. 2023) and heterogeneity (Jarzyna et al. 2014). However, we have so far lacked any general framework for parameterizing and estimating the dynamic imprints of assembly processes and environmental factors on community dissimilarity from empirical data (Ferrier et al. (2007) for adaptive responses and Jarzyna et al. (2014) for spatially varying responses).

A resolution of temporal and spatial shifts in the drivers of community dissimilarity is needed for a new understanding of community dynamics under heterogeneous change in multiple environmental properties. For example, understanding how the drivers of spatial dissimilarity of communities vary across years will inform us about the stability of and possible regime shifts in community dynamics (Pedersen et al. 2020). Analogously, pinpointing spatial variability in the drivers of temporal dissimilarity will inform us about latitudinal shifts and site-specificity in community processes (Soininen et al. 2007, Qian et al. 2008). Moreover, spatial and temporal turnover can be driven by different processes (for example He et al. 2023 for spatial turnover and Daskalova et al. 2020 for temporal turnover). Hence, resolving turnover along both the spatial and temporal dimensions can resolve different assembly processes and highlight differential levels of variability in space and time. Moreover, they can help us identify the current drivers of change and thus suggest what corrective measures are needed to mitigate local change.

To narrow the current knowledge gap, we introduce the concept of non-stationary community responses to assembly processes and environmental factors. With a non-stationary response, we refer to a model structure which allows the response to a covariate to vary between modeling units, such as time points (monitoring years) or study cells (monitoring sites), while assuming dependence between the temporal or spatial units through a covariance structure. This concept allows us to estimate the effects of assembly processes and environmental factors on community dissimilarity at the level of a single year or a locality, then scaling them up to the decadal or regional extent, respectively. This approach offers a largely untapped opportunity for community ecology (Declerck et al. 2011, Henriques-Silva et al. 2013, Jabot et al. 2020), and provides an attractive analytical solution to exploring the drivers of diversity patterns across scales (called for already in McGill et al. (2015)).

In the current contribution, our objective is to test for the existence of non-stationary responses of spatial and temporal community dissimilarity. We apply them in assessing temporal regime shifts in spatial community dissimilarity and latitudinal trends and site-specificity in the imprints of different forces on temporal community dissimilarity. To demonstrate differences in inference, we also compare the non-stationary responses resolved to the imprints inferred based on conventional, stationary responses.

To resolve the relative imprints of different forces, we need a coherent framework for categorizing the processes driving dissimilarity in community composition. To this aim, we adopt the widely-used metacommunity framework (Leibold et al. 2004, Cottenie 2005, Myers et al. 2013). In this framework, assembly processes are grouped into four 'archetypes' or 'paradigms': species sorting, neutral dynamics, patch dynamics and mass effects. Environmental filters reflect the imprint of species sorting, as communities are assumed to be a product of species' ecological niches. This paradigm postulates a decrease in the similarity of communities with increasing environmental distance between them (Cottenie 2005, Leibold and Loeuille 2015). We further group neutral and patch dynamics into the joint concept of 'random processes', as they will produce a decrease in the similarity of communities with increasing spatio-temporal distance between them, without any need for an external driver (Cottenie 2005, Gravel et al. 2010). To quantify the relative contributions of environmental filtering versus random processes, we characterize environmental filters by climate and land cover – as these factors have been found to be the most important systematic drivers of community composition in our study groups (Virkkala et al. 2004, Virkkala and Lehikoinen 2014 for birds; Kuussaari et al. 2007 for butterflies; Pöyry et al. 2011 for moths) – with added imprints of random processes. By applying non-stationary responses we ask how strong are the imprints of environmental filtering related to climate and land cover and of random processes on species communities in a boreal ecosystem. Hence, we test the community-level environmental relationships examined by (Virkkala et al. 2004, Kuussaari et al. 2007, Pöyry et al. 2011, Virkkala and Lehikoinen 2014, Jaureguiberry et al. 2022) and reveal the non-stationarity of such relationships.

At the focus of our analyses are multidecadal community responses among bird, butterfly, and moth communities in Finland. These data are massively replicated in space and time, and cover 340 000 km^2, 11° of latitude and 22–42 years of observations (depending on the species group; Fig. 1). We characterize community dissimilarity per species group by computing pair-wise Bray–Curtis dissimilarity, i.e. beta-diversity, between each monitoring site and year (Fig. 1B). We then relate community dissimilarity to differences in climate and land cover, as well as to spatial and temporal distance between the communities with non-stationary responses (Fig. 1D). We estimate the associations between community and environmental change as spatially or temporally varying covariate effects and apply the varying coefficient methodologies from Jarzyna et al. (2014) and Doser et al. (2024a, 2024b). In our current approach, we focus purely on the factors creating cumulative dissimilarity in communities. For clarity, we note that we explicitly overlook other types of stochastic factors, such as demographic stochasticity, as they create non-directional variation in a community. Hence, throughout the text, we will explicitly refer to non-stationary responses – rather than to e.g. context-dependency, which is frequently used as a catch-all descriptor of 'all sorts of factors shaping different communities in different directions'.

For each species group we ask:

1. What are the relative imprints of environmental filtering with climate and land cover as its major components and random processes on the community dynamics?
2. Do non-stationary responses resolve patterns in community responses hidden by stationary models?
3. Do non-stationary responses reveal:
   (a) regarding spatial dissimilarity, regime shifts in time (i.e. a shift from the dominance of one driver to another)?
   (b) regarding temporal dissimilarity, regime shifts along a latitudinal gradient?

In assessing the patterns, we made two a priori predictions: First, we expected higher non-stationarity in the drivers of temporal than spatial dissimilarity – since changes in local land cover over time can create strong dissimilarity in a community (as shown by Jarzyna et al. 2014) compared to the smoother imprints of gradual climate change (Rantanen et al. 2022). Second, we expected spatial community dissimilarity to be more strongly associated with environmental filtering and temporal community dissimilarity with random processes. This is because climate gradients occurring over Finland are relatively long and steep compared to the temporal climate gradients over the monitoring period. However, we expected to see a gradually increasing imprint of climate on spatial community dissimilarity during the monitoring period, as a result of the intensification of climate warming (Rantanen et al. 2022).

Material and methods

Species data

To compare drivers of community dissimilarity in space and time, we drew on long-term systematic monitoring data of birds, butterflies (day active Lepidoptera), and moths (night active Lepidoptera) sampled across Finland (60°N–70°N, 19.4°E–31°E), covering four bioclimatic zones from southern to northern boreal zone (Fig. 4). All species groups were surveyed following standardized monitoring protocols (Lehikoinen 2012, Virkkala and Lehikoinen 2014) for birds, (Kuussaari et al. 2007, Heliölä et al. 2022) for butterflies and (Leinonen et al. 2016, 2017) for moths. Birds were monitored along 1147 three to six kilometer long line transects 1978–2020, including 145 species recorded. Butterflies were monitored in 101 one to three kilometer long line transects 1999–2020, including 92 species recorded. The lengths of the bird and butterfly transects varied randomly between sites and thus did not introduce bias in the model estimates. The butterfly transects cover 5–20 different habitats and thus the transects differ in terms of habitat heterogeneity. The number of surveys per butterfly transect and per year varied also. This systematic difference between transects has been accounted for in the analysis and explained in detail in the section on analysis and model fitting. Moths were monitored with stationary moth traps in 99 sites 1993–2018 including 908 species recorded.

For butterflies and moths, the communities are monitored throughout the active period of the species (spring–autumn). Birds are monitored during a single visit per year during the peak of the singing season (June–July). The timing in relation to active flying and singing seasons ensures that most of the species present at the monitoring sites are recorded.

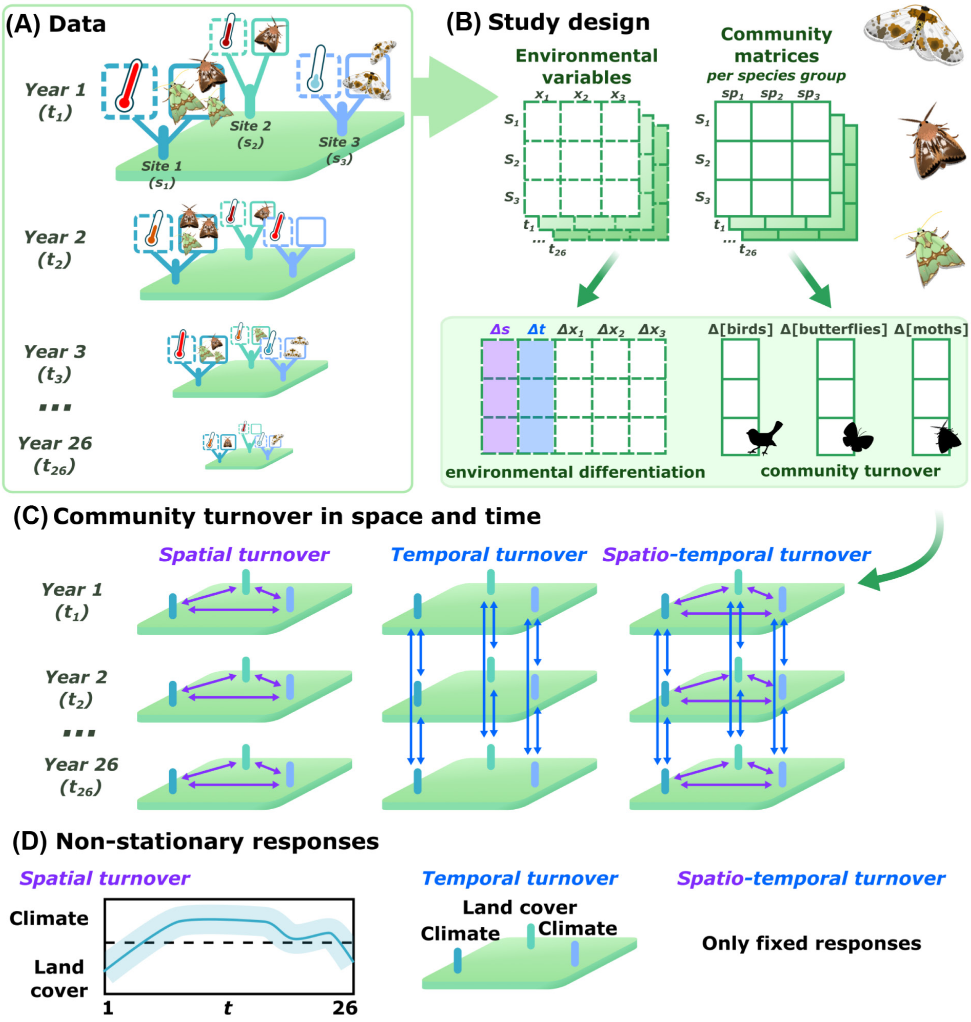

Figure 1. A representation of the study design and the distribution of species and environmental data. (A) shows the concept of spatio-temporally distributed community and environmental data. Here, a moth community has been monitored along with the environment in three study sites for 26 years. In (B), the monitoring program creates a time-series of community composition and environmental conditions for each study site. We build pair-wise comparisons between survey sites and associate the Bray–Curtis dissimilarity of species communities (Δ species group) to differences in spatial location (Δs), time (Δt) and environmental (Δx) variables. (C) shows our approach to studying spatio-temporal community dissimilarity and how we break it to purely spatial and temporal compartments. (D) illustrates the idea of non-stationary responses for spatial and temporal community dissimilarity. First, the importance of climate and land cover for spatial community dissimilarity is allowed to vary over the monitoring years. Second, the same is done for temporal community dissimilarity over the monitoring sites.

Community data were pooled per species group at the level of a year and a site, thus summing all recorded species abundances within the samples of that year. Since the monitoring covers the phenological cycle and community turnover during a year, the resulting year-level sums reflect the total abundance of a species independent of their phenological cycles.

The sampling methods did not change during the monitoring period, but some of the monitoring sites changed when some were discarded and new ones adopted. However, the placement of monitoring sites was spatially balanced throughout the overall monitoring period (described by Kuussaari et al. 2007, Leinonen et al. 2017, Heliölä et al. 2022 for butterflies and moths; Lehikoinen 2012 for birds). On average, sites were monitored for 3.14 years for birds, 9.97 years for butterflies, and 12.8 years for moths. The monitoring sites spanned a latitudinal gradient of 10.26° for birds, 6.21° for butterflies, and 9.39° for moths. For full details on the taxon-specific data, see the Supporting information, and for the temporal and spatial distribution of monitoring sites see Fig. 4, Supporting information). Importantly, the sampling effort is identical between years and sites within species groups. This ensures that the observed community turnover between the monitoring sites and years reflects the impact of environmental and stochastic drivers instead of the sampling effort. Thus, inference of community turnover provides unbiased estimates of environmental and stochastic drivers.

Climate data

We characterized the climate of the monitoring sites through temperature, precipitation, and snow cover, all commonly pinpointed as key drivers of population and community dynamics in Northern Europe (for birds Virkkala and Lehikoinen 2014, Fraixedas et al. 2015, Hällfors et al. 2020, Deshpande et al. 2022, Bosco et al. 2023, butterflies Luoto et al. 2006, Kuussaari et al. 2007 and moths Kuussaari et al. 2007, Pöyry et al. 2011). Thus, for each site and year, we calculated the heat and precipitation sums of the growing season, the number of freezing days, and the duration of snow cover in days. These environmental covariates were calculated per year, so that the heat and precipitation sums described the conditions of the sampling season, and the freezing days and snow cover duration described the previous winter. The variables were derived from daily records of mean temperature, the sum of precipitation, and the depth of snow cover provided at a resolution of 10 × 10 km by the Finnish Meteorological Institute (Aalto et al. 2016).

The temporal scale of the climatic variables has been set to match the annual resolution of the survey data. The climatic variables reflect the conditions during both winter and the growing season. For variables reflecting the full growing season, such as the temperature sum accumulated, some early species will experience only part of the conditions. Still, as we pool the local data over the whole annual survey period, we cannot vary the seasonal coverage of the environmental variables for certain parts of the community. We expect this solution to create some uncertainty but no major bias in the estimates. In our final comparisons (i.e. those between environmental filtering versus random processes, and between climate versus land cover) and conclusions, we account comprehensively for all inherent uncertainties.

Land cover data

Land cover data were derived from the Corine Land Cover of 2000, 2006, 2012 and 2018, which classifies land cover into 44 classes at a 25 × 25 m resolution across Europe (EEA 2000, 2006, 2012, 2018). To characterize the land cover around the monitoring sites, we defined a 500-m buffer around the site for moths and butterflies and a 1-km buffer for birds (as reflecting the higher mobility of birds). The buffers were chosen based on earlier studies applying a similar study setting or explicitly testing different buffer zones (for birds LeBrun et al. 2016, Veech et al. 2017, Santangeli et al. 2023, Nereu et al. 2024; for butterflies and moths Archaux et al. 2018, Kasiske et al. 2023, Nereu et al. 2024). Here, the site coordinates were set to the center point of a monitoring transect for birds and butterflies and to the trap location for moths. Within the buffer, we characterized the land cover for all species groups as the proportions of broad leaf (class 311 in the Corine Land Cover data set), coniferous (class 312), and mixed forests (class 313); pastures (231); patchy agricultural areas (243); grasslands (321); and patchy woodlands (324). We summed pastures and patchy agricultural areas to reflect semi-open to open agricultural areas, and grasslands and patchy woodlands to reflect semi-open to open non-agricultural areas. This set of land cover variables is supported by earlier studies for the species groups (for birds Heikkinen et al. 2004, Virkkala et al. 2004, Luoto et al. 2007; for butterflies Luoto et al. 2006, Kuussaari et al. 2007; for moths Kuussaari et al. 2007). As a measure of land cover variability, we used the concept of entropy – a measure commonly used in spatial statistics to quantify the general evenness of different land cover classes (Carranza et al. 2007). For all species groups, entropy was defined over all land cover classes inside a buffer:

$$H(l) = -\sum_{j=1}^{J} p(l_j)\log(p(l_j)) \tag{1}$$

where H is entropy, l is land cover, j is a subindex for a land cover class, J is the number of different land cover classes within a buffer and p(l) is the proportion of coverage of the land cover class within a buffer.

We acknowledge that the climate and land cover data came with different spatial resolutions. However, introducing covariates at different resolutions does not automatically create uncertainty – as long as the resolutions used reflect the distances at which the respective environmental factor varies in nature. From this perspective, a 10 × 10 km resolution for a climate layer appears relatively high when compared to the overall variation in macroclimate across the study region and is comparable to the resolution in climate layers from CHELSA (Karger et al. 2023) and WORLDCLIM (Fick and Hijmans 2017), which are commonly applied in ecological research. For the current analyses, we expect that the resolution of the climate data will suffice to capture the variation relevant to the species communities. Moreover, the buffering of land cover information (using a 0.5–1 km buffer; above) brought the realized resolution of land cover data closer to that of climate data.

Since species monitoring periods start before the first land cover survey, we assigned the value of NA to the land cover variables for all monitoring sites prior to 2000, while noting that this approach can increase uncertainty for the estimates of the land cover effects. From 2000 onward, we assigned a linearly interpolated value of the land cover values for each year that falls between the survey years (2000, 2006, 2012, and 2018). For linear interpolation, we used the values from the preceding and following surveys. For the years 2019 and 2020 we fixed the values to those observed during the 2018 survey.

Community dissimilarity and environmental association

We applied abundance-based dissimilarity metrics for measuring the proportional changes among species communities and capturing variation associated with, e.g. the stochastic occurrence of rare and low-abundance species in survey data. Such species are typical of highly diverse communities including moths (Fisher et al. 1943). We quantified community dissimilarity by calculating pairwise Bray–Curtis dissimilarity between the communities observed at each site in each year. Bray–Curtis distance (BC) between two sites j and k is defined as $\mathrm{BC}_{j,k} = 1 - \dfrac{2 \times \sum_{i=1}^{I} \min(N_{i,j}, N_{i,k})}{\sum_{i=1}^{I} \min(N_{i,j}, N_{i,k})}$, where $N_{i,j}$ is the abundance of species i at the site j and $N_{i,k}$ the abundance of species i at the site k. Hence, BC quantifies the dissimilarity between two community compositions on the level of individuals. BC varies between 0 (the same species with the same abundances between sites) and 1 (no shared species between sites).

Environmental variation was characterized by computing Euclidean dissimilarity for environmental conditions and sampling effort (for butterflies) between each site and year. Dissimilarities were calculated specifically for each climate and land cover variable. For butterflies, we characterized sampling effort with the number of visits and the number of different habitat segments per transect and year. As birds were surveyed by visiting an active site once per year, there was no variability in survey effort between active sites (Virkkala and Lehikoinen 2014). Lastly, we accounted for the different community sizes and the nestedness pattern of abundant species (Baselga 2010) by computing the pairwise difference in species richness between sites and using that as an explanatory variable in the models.

We characterized random processes (i.e. neutral dynamics + patch dynamics) with the spatial and temporal distances between each site and each year. Spatial and temporal distances reflect spatially and temporally structured processes that are not necessarily associated with environmental variables, such as dispersal.

Our approach allowed us to study community dissimilarity in a spatio-temporal context and to partition the spatio-temporal dynamics into pure spatial and temporal components (Fig. 1C). Specifically, the purely spatial and temporal components were derived by filtering the community and environmental dissimilarity data to either include only pair-wise comparisons for which the temporal distances were zero (for spatial dynamics) or for which the spatial distances were zero (for temporal dynamics).

Given that we had in total ten explanatory variables, there is a risk of collinearity between the covariates. To address this concern, we computed Pearson correlation coefficient between covariates for each species in spatio-temporal, spatial, and temporal dissimilarity settings. We found a remarkable correlation (> 0.7, adopted as a practical threshold identified by Dormann et al. 2013) between coniferous and mixed forests for butterflies in the context of spatio-temporal (coefficient 0.74) and spatial (coefficient 0.87) dissimilarity. Since these two correlations were the only ones exceeding 0.7 among the 495 correlations examined, they have no major impact on our analyses or conclusions. Moreover, as we accounted for posterior correlation between covariate effects, the increase in uncertainty resulting from collinearity is comprehensively propagated to the final comparisons made between the imprints of environmental filtering versus random processes and of climate versus land cover.

Analysis and model inference

To extract the spatio-temporal, purely spatial and purely temporal dimensions of community dissimilarity, we fit a total of five models for each species group separately (Table 1): one for assessing spatio-temporal community dissimilarity (model 1 with spatio-temporally stationary responses), two for assessing spatial community dissimilarity (model 2 with temporally stationary responses and model 3 with temporally non-stationary responses), and two for assessing temporal community dissimilarity (model 4 with spatially stationary responses and model 5 with non-stationary varying responses).

In each model, we regressed the log-transformed Bray–Curtis dissimilarity values against log-transformed dissimilarity values of climate, land cover, species richness, spatial and temporal distance variables (as applied in Soininen and Hillebrand 2007). For butterflies, we also added a log-transformed variable reflecting difference in sampling effort (number of visits and habitat segments in a site in a year). The linear predictor for the models 1, 2 and 4 (stationary responses) was defined as

$$y_i(x_i) = \alpha + \sum_{j=1}^{J} \beta_j x_{i,j} + \varepsilon_i \qquad (2)$$

where y_i is the i:th sample of log-transformed Bray–Curtis distance, x_i is a collection of log-transformed environmental, spatial and temporal dissimilarity values of length J, α is a model intercept, β_j is a linear weight for the j:th variable and ε_i is a random error term. All variables were scaled to a zero mean and a standard deviation of one, thereby making their estimated effects comparable. The estimates for the β_j correspond to the importance of the respective environmental, spatial or temporal variable for the community dissimilarity. For models 2–5, we included random effects to explain the additional temporal or spatial variability that is not associated with any explanatory variable (below for a more thorough presentation of the random effects). In models 2 and 3 for spatial dissimilarity, we included a temporal first-order random walk. In models 4 and 5 for temporal dissimilarity, we included a Besag-type conditional autoregressive spatial random effect.

Linear combinations

The comparison between the categories of environmental filtering and random processes was conducted by taking linear combinations of the covariate effect estimates. We computed environmental filtering by summarizing the estimates for climate and land cover variables. We computed random processes by summarizing the estimates for the variables corresponding to spatial and/or temporal distances. The difference between the categories was estimated by subtracting the sum effect of random processes from the sum effect of environmental filtering. The difference between the effects is here called their linear combination (LC) and defined as

$$LC \sim N(X_D \tilde{\mu}, X_D, \Sigma X_D^T) \quad (3)$$

where $\tilde{\mu}$ is a vector collecting estimates for the covariate effects, and Σ is a variance-covariance matrix of the joint posterior probability distribution of the covariate effects. X_D is a design matrix with as many columns as there are explanatory variables and only one row, which defines the covariate comparison. For comparing environmental filtering and random processes, X_D has a value of (1) for the environmental covariates and (−1) for the variables corresponding to spatial and/or temporal distances. For comparing climate and land cover, X_D has (1) for climate covariates and (−1) for land cover covariates. Covariates irrelevant to the linear combinations, such as survey effort, were assigned zeros. The size of the vector $\tilde{\mu}$ is the number of explanatory variables. Effectively, generating such a linear combination equals summarizing the estimated effects of the covariates belonging to two categories and subtracting the sum effect of the second category from the sum effect of the first category. Positive estimates for linear combinations indicate higher importance of environmental filtering over random processes (comparison 1) and of climate over land cover (comparison 2).

In both comparisons, we assess the differences between the marginal effects of the covariates. If we had not accounted for the collinearity between covariates by estimating posterior correlations of the covariate effects, we would end up with overly large uncertainties for the comparisons. By accounting for these posterior correlations, we can address the difference between the effects of covariate categories more precisely. The resulting comparison closely aligns with the idea of Cottenie (2005), who proposed establishing the difference between the mutually independent effects of environmental filtering and random processes or climate and land cover.

Non-stationary responses

For the models assuming non-stationary responses, we replaced the term β_j in Eq. 2 with a temporally non-stationary response $\beta_{j,t}$ (model 3) or a spatially non-stationary response $\beta_{j,s}$ (model 5). Especially spatially non-stationary responses have gained much attention in ecological modeling of species distributions (Thorson et al. 2023, Doser et al. 2024a, 2024b) and community dissimilarity (Jarzyna et al. 2014). As there is substantial literature on their development (Gelfand et al. 2003) and use (Doser et al. 2024a, 2024b), our main achievement is in scaling them to simultaneous estimation of multiple covariate effects, and of broader categories consisting of multiple, biologically-related variables, rather than in developing a whole new family of models.

We modeled temporally non-stationary response as a first-order random walk so that

$$\beta_{j,t} \sim N(\beta_{j,t-1}, \pi_j^{-1}) \quad (4)$$

where π denotes random variability between two consecutive time points. Thus, we get $\beta_{j,t} + \beta_{j,t-1} + \omega_{j,t}$, where $\omega_{j,t} \sim \pi_j^{-1}$ (Blangiardo et al. 2013, Bakka et al. 2018). Note that π was estimated along with the responses but is not of primary interest for our current hypothesis testing. Following the INLA-procedure we set a penalized complexity prior for each π^{-1} so that with probability 0.99 they are smaller than 1. We defined the temporally varying covariate effects on a one-year resolution and thus allowed the estimates to vary from year to year.

The spatially non-stationary response was modeled as a Besag-type random effect, which models the response of community dissimilarity to explanatory variables as an average of responses of the adjacent monitoring sites (Besag et al. 1991). The response at the monitoring site given the adjacent monitoring sites was defined as

$$\beta_{j,s} \Big| \beta_{j,-s} \sim N\left(\mu_{j,s}, Q^{-1}\right) \quad (5)$$

where $\mu_{j,s}$ is the average of the responses in the spatially adjacent monitoring sites $\frac{\sum_{n=1}^{N_s} \beta_{j,n}}{N_s}$ and Q^{-1} is the precision proportional to the number of adjacent monitoring sites multiplied by the precision parameter $Q^{-1} = \frac{1}{N_s \tau}$. Here, N_s is the number of adjacent monitoring sites to the focal monitoring site (s) and τ is the precision parameter. We assigned a log-gamma prior on log(τ) so that log(τ) ~ log − gamma(.1,.1). We defined the adjacency matrix with the k-nearest neighbour method by fixing the number of neighbors per monitoring site to six. For computing the adjacency matrix, we used the *chooseCN* function of the 'adegenet' (Jombart 2008) R package (ver. 2.1.8).

The linear combinations of the temporally non-stationary estimates were derived at the level of a year for temporally non-stationary models (model 3) and at the level of monitoring sites for spatially non-stationary models (model 5). We computed linear combination for non-stationary models following the same approach as used for computing linear combinations for models with stationary effects over years and sites. However, the vector $\tilde{\mu}$ corresponds to the temporal average in the case of spatial dissimilarity (model 3) and spatial average in the case of temporal dissimilarity (model 5). Regarding non-stationary models, we computed linear combinations for each monitoring year in the case of spatial dissimilarity (model 3) and monitoring site in the case of temporal dissimilarity (model 5). Hence, we could produce temporally and spatially explicit examinations in addition to the general examination. We captured the full uncertainty of the linear combinations by propagating uncertainty from posterior distributions of model parameters and accounting for the temporal and spatial correlations between monitoring sites and years.

Model fitting

All models were fitted with hierarchical Bayesian inference using 'INLA' package (ver. 22.05.07) in R (ver. 4.2.1; www.r-project.org). To provide model fit diagnostics for model selection over stationary and non-stationary models, we compared them in terms of the negative expected log posterior predictive density (−E[LPPD]) (Vehtari et al. 2017). We utilized the conditional predictive ordinate -values (CPO) from of the models fitted with INLA. The data point specific CPO values correspond to the probability of observing the respective value of the response variable if introducing the data point only to model validation. We summarized the CPO values for a model by taking the negative of the mean of logarithmic scores –E(log(CPO)). A smaller value denotes a better model fit.

Results

Environmental variability

The environmental change recorded across space and time differed among species groups, as due to the different monitoring period and placement of monitoring sites for different species groups (Fig. 3, Supporting information). Between monitoring sites within a study year, the heat and precipitation sums of the growing season varied by an average of 1273°C and 388 mm for birds, by 819°C and 251 mm butterflies and by 1282°C and 427 mm for moths, respectively. The coverage of most land cover classes varied from full coverage to an almost complete absence for all species groups.

Across study period and monitoring sites, heat and precipitation sum of the growing season changed on average per monitoring year by 7.05°C and 2.48 mm for birds, 0.42°C and 1.73 mm for butterflies and 13.72°C and −0.13 mm for moths, respectively. Simultaneously, average changes in the coverage of different land cover classes were between zero and three percentage for all species groups. However, there was large variability between the monitoring sites in land cover changes (Supporting information).

Spatial dissimilarity

The average spatial Bray–Curtis dissimilarity per year varied between 0.38 and 0.44 for birds, between 0.50 and 0.52 for butterflies and between 0.67 and 0.68 for moths (Supporting information:). These numbers reflect the positive effect of species pool size on community differentiations (145 birds species, 93 butterfly species and 890 moth species) and higher levels of variability of insect compared with vertebrate communities.

To characterize differences in the imprints of environmental filtering (climate and land cover) versus random processes (spatial distance), we used the linear combination (LC) ($\beta_{\text{climate + landcover}} - \beta_{\text{spat.distance}}$). Here, positive values denote a larger imprint of environmental filtering, whereas negative values denote a larger imprint of random processes. We applied the same approach to compare the imprints of climate (reflected by positive LC) and land cover (reflected by negative LC). Overall, models assuming stationary and non-stationary responses showed consistent results for spatial community dissimilarity across species groups, with a larger average imprint of environmental filtering than of random processes among birds (where the LC of the stationary model was 0.38 and of the non-stationary model 0.24, both $p < 0.05$), butterflies (LC of the stationary model 0.14; non-stationary model 0.12, both $p < 0.05$) and moths (LC of the stationary model 0.12; non-stationary model 0.16, both $p < 0.05$) (Fig. 2A, C). However, the average response estimated by the temporally non-stationary model varied during the study period between −0.21 and 0.72 for birds, between −0.22 and 0.45 for butterflies and between −0.35 and 0.39 for moths (Fig. 2E). For birds, we found a declining trend in the imprint of environmental filtering.

Climate left a larger imprint than land cover on community dissimilarity among birds (LC of the stationary model was 0.09 and of the non-stationary model 0.35, both $p < 0.05$). For butterflies, the relative imprints of climate and land cover were associated with major uncertainty when estimated by the stationary model (LC 0.03, $p > 0.05$), whereas the non-stationary model resolved a larger imprint of climate (LC 0.07, $p < 0.05$). For moths, the LC was associated with major uncertainty in both the stationary and non-stationary models (0.01 stationary model and -0.03 non-stationary model, both $p > 0.05$) (Fig. 2B, D). Across the study period, the average LC varied substantially (Fig. 2F). For birds, average LC varied between 0.13 and 0.62, between −0.14 and 0.44 for butterflies, and between −0.17 and 0.08 for moths, with matching variation in the associated uncertainty. For butterflies and moths, the imprint of climate strengthened consistently after 2013, indicating a shift towards a dominant role of climatic filtering.

Temporal dissimilarity

The average temporal Bray–Curtis dissimilarity per site was lower than the year-level average spatial dissimilarity: 0.22 for birds, 0.32 for butterflies and 0.44 for moths. The site-level averages varied between 0.15 and 0.30 for birds, 0.28 and 0.37 for butterflies and 0.37 and 0.49 for moths (Supporting information). This reflects the long latitudinal gradient along which communities differentiate more than during the study period.

For temporal dissimilarity, we found larger inconsistencies between stationary and non-stationary models than for spatial dissimilarity (above). This difference was largely due to the large spatial variance in the imprints of assembly processes and environmental variables among monitoring sites (Fig. 3).

Stationary models supported a larger imprint of random processes than of environmental filtering, with an average LC of −0.49 for birds, −0.28 for butterflies and −0.44 for moths (all $p < 0.05$; Fig. 3A). In the non-stationary model, the average LC was associated with major uncertainty for birds (−0.03, $p > 0.05$) and butterflies (0.24, $p > 0.05$). However, for moths the estimates of the non-stationary model were consistent with those from the stationary model (average LC −0.51, $p < 0.05$; Fig. 3C). Regarding the comparison between the imprints of climate and land cover, stationary models supported a larger imprint of climate for all species groups with average LC 0.04 for birds, 0.08 for butterflies

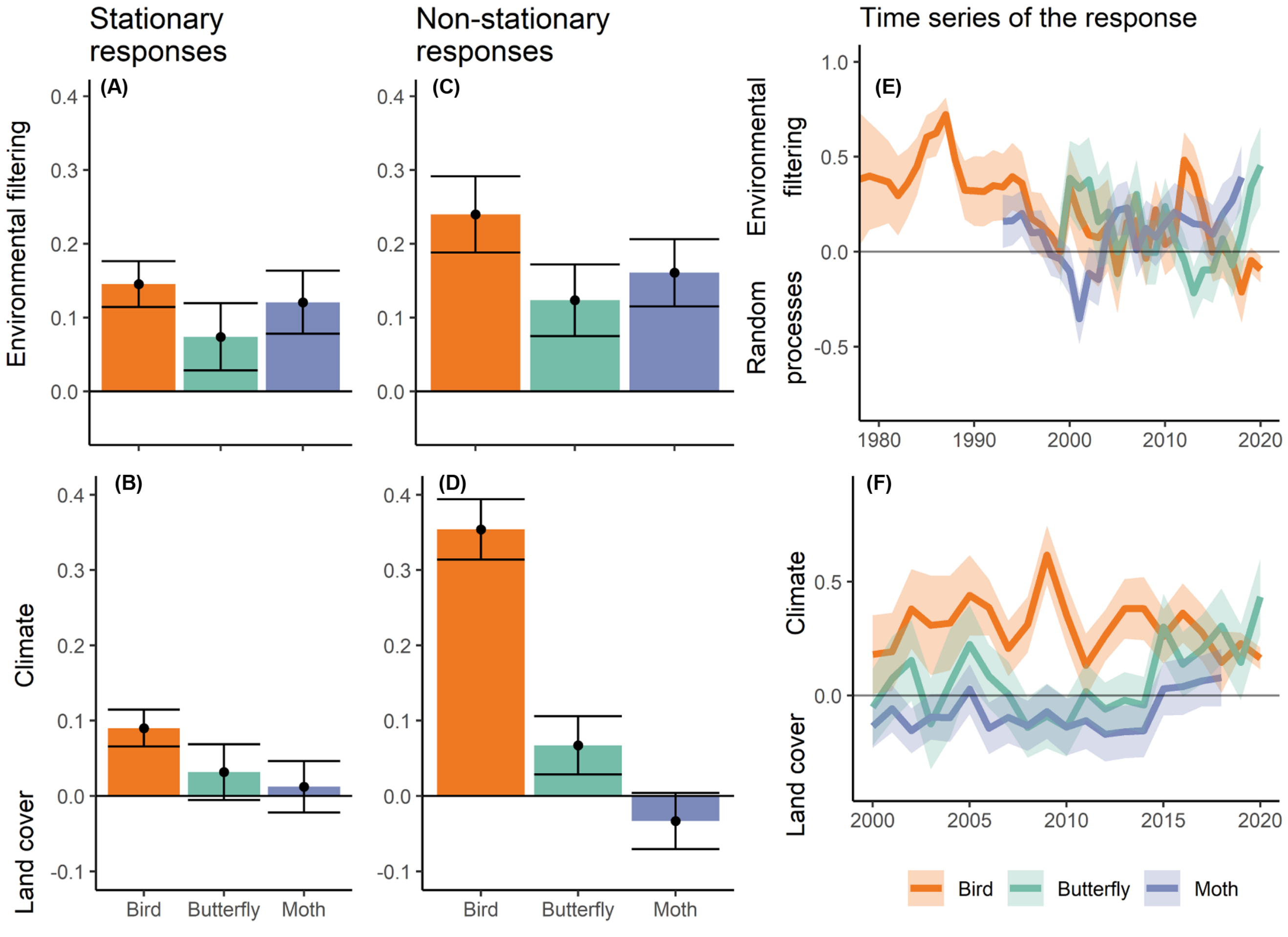

Figure 2. Average imprint of environmental filtering versus random processes (upper panels) and climate versus land cover (bottom panels) for spatial dissimilarity in stationary (A)–(B) and non-stationary models (C)–(F). For climate-land cover comparison, the mean values are computed over the years since 2000 as there is no land cover data for those years. In panels (A–D), bars and dots denote the mean and error bars denote the 95% credibility intervals. On the y-axis, positive values denote larger imprints of environmental filtering (A), (C) and climate (B), (D). For plots (A) and (C), we cut out the space below zero, which would represent random processes. In panels (E) and (F), the line denotes the mean estimate with 95% credibility interval presented as the shading around it. In plot (F), we cut out the years prior to 2000. All species groups are associated with environmental filtering though with annual variability. Climate is more important than land cover for birds and butterflies. The average imprints of climate versus land cover on butterflies and moths switches consistently from the domination of land cover to that of climate after 2013.

and 0.15 for moths (all $p < 0.05$; Fig. 3B). Contrary to the stationary model, non-stationary model supported a larger imprint of land cover than of climate for birds (average LC −0.39, $p < 0.05$) and butterflies (average LC −0.47, $p < 0.05$; Fig. 3D). For moths, the non-stationary model agreed with the stationary model in identifying a larger imprint of climate (average LC 0.17, $p < 0.05$) than of LC (Fig. 3D).

Inflated uncertainty in the average LC of the imprint of environmental filtering versus random processes was due to the large spatial variance of the respective site-level LC. Site-level average LC varied among monitoring sites between −2.4 and 3.03 for birds, −0.91 and 2.16 for butterflies and −2.00 and 0.23 for moths (Fig. 3E, G, I). Regarding the LC of the imprints of climate versus land cover, average LC among monitoring sites varied between −3.63 and 2.11 for birds, between −2.33 and 0.39 for butterflies, and between −0.51 and 1.40 for moths (Fig. 3F, H, J).

Along the latitudinal gradient, we found distinct patterns among species groups in site-level average LC. For birds, the site-level average LC followed a complex pattern, crossing zero at least twice in comparisons for environmental filtering versus random processes and climate versus land cover (Fig. 5). For butterflies, the site-level average LC flipped at 61°N from showing a larger imprint of environmental filtering over random processes to suggesting the opposite, with a simultaneous decline in the imprint of land cover over climate. Nonetheless, the average LC did not flip to support a larger imprint of climate (Fig. 5). For moths, the site-level average LC stayed unchanged, overall supporting larger imprints of random processes and of climate (Fig. 5).

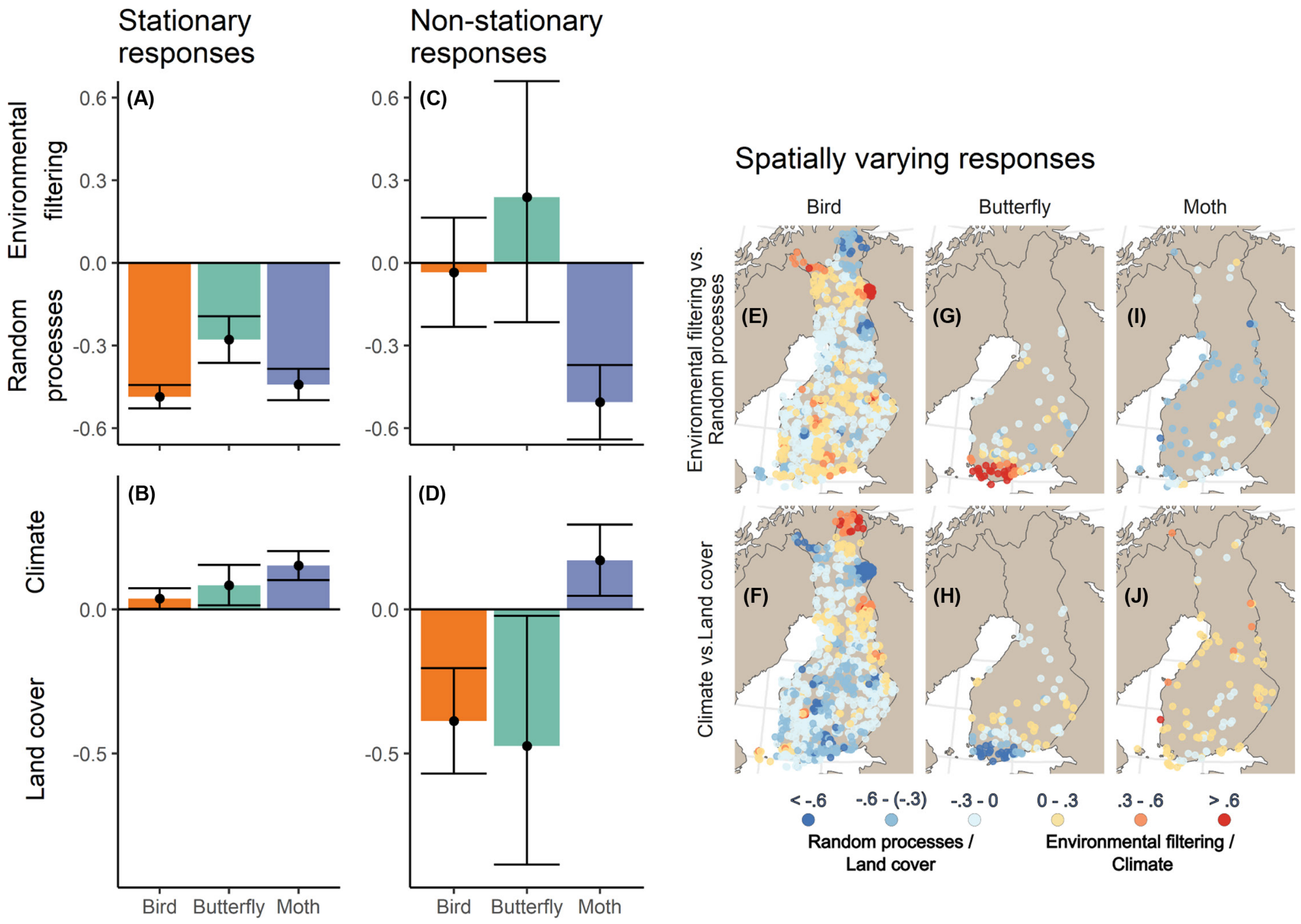

Figure 3. Average imprint of environmental filtering versus random processes (upper panels) and climate versus land cover (bottom panels) for temporal dissimilarity in stationary (A)–(B) and non-stationary models (C)–(J). In panels (A)–(D), bars and dots denote the mean and error bars denote the 95% credibility intervals. On the y-axis, positive values denote larger imprints of environmental filtering (A), (C) and climate (B), (D). In plots (E)–(J), points represent monitoring sites on the maps. Red points denote larger imprint of environmental filtering compared to random processes and of climate compared to land cover, whereas blue points denote the opposite. Stationary models strongly support random processes and climate as the major drivers of community change. In non-stationary models, the responses of birds and butterflies to environmental filtering and random processes varied geographically creating highly uncertain average responses. The responses of moths possessed less geographical variation with a consistently larger imprint of random processes. Land cover had a larger imprint on birds and butterflies though again with large geographical variability. Climate had a larger imprint on moths than what land cover had.

Spatio-temporal dissimilarity

We finish the results by comparing the purely spatial and temporal components of community dissimilarity to their combination as spatio-temporal dissimilarity. Bray–Curtis dissimilarity in the spatio-temporal study setting was lowest for birds (average 0.48; 95% credibility interval (CI): 0.39–0.56), followed by butterflies (average 0.58; 95% CI: 0.51–0.64) and moths (average 0.74; 95% CI: 0.70–0.78; Supporting information).

The estimates for the imprints of assembly processes and environmental variables for spatio-temporal dissimilarity are not straightforward but more like haphazard compromises between the respective estimates for spatial and temporal dissimilarities. Random processes had a larger imprint than environmental filtering had on the community dissimilarity of bird (average LC: -0.09, $p < 0.05$) and moth communities (average LC -0.09, $p < 0.05$), whereas imprints on butterfly communities were associated with wide uncertainty (average LC 0.01, $p > 0.05$; Fig. 4A). Climate left a larger imprint than land cover on the dissimilarity of bird communities (average LC 0.08, $p < 0.05$) and butterflies (average LC 0.02, $p < 0.05$), whereas land cover left a larger imprint on moth communities (average LC -0.15, $p < 0.05$; Fig. 4B).

Model comparison

Overall, model comparison based on model fit showed that non-stationary models performed better than the stationary models in explaining spatial and temporal community dissimilarity for all species groups (Table 1).

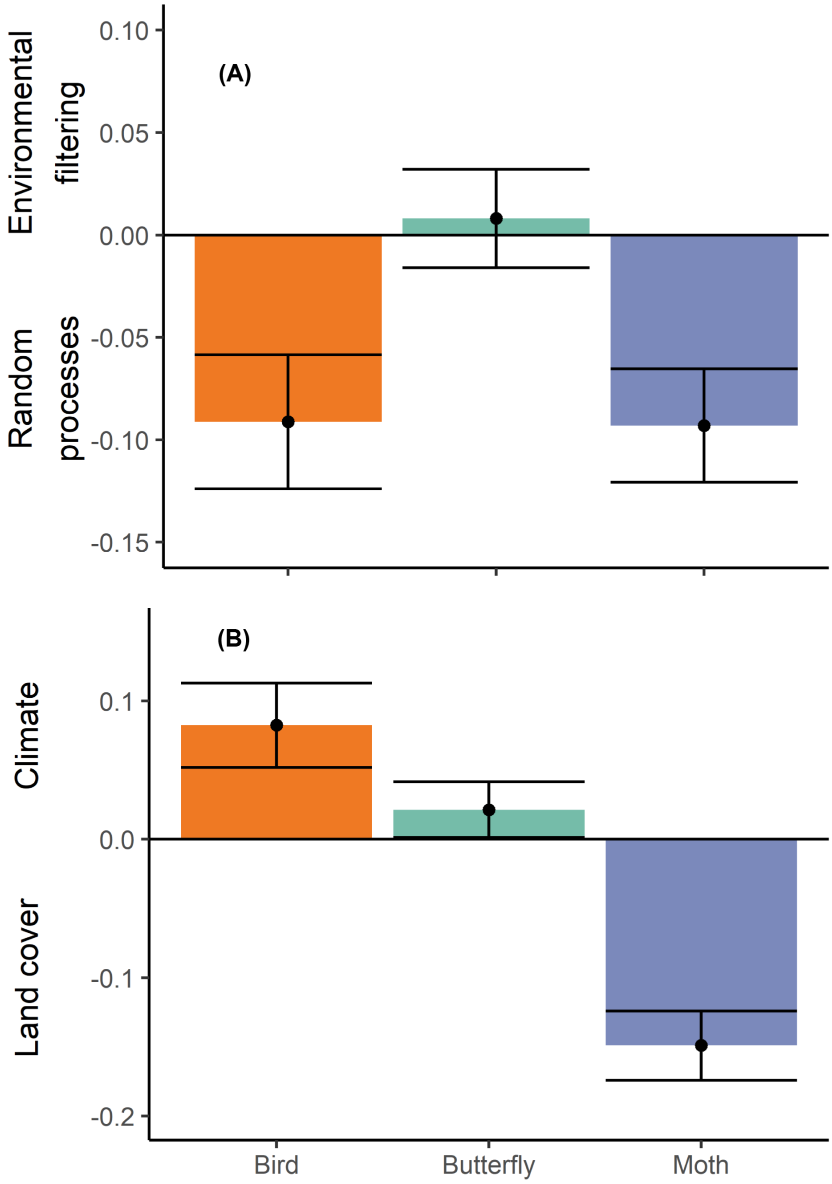

Figure 4. Average imprint of environmental filtering versus random processes (A) and climate versus land cover (B) for spatio-temporal dissimilarity. Panels lay out the mean value (bar and point) and 95% credibility intervals. Positive values denote a larger imprint of environmental filtering or climate and negative values denote a larger imprint of random processes or land cover. Spatio-temporal dissimilarity is either relatively weakly associated with random processes (birds and moths) or uncertain in terms of 95% credibility interval (moths). Climate is more important than land cover for birds and butterflies.

Discussion

In this paper, we have revealed complex imprints of different forces on spatial and temporal community dissimilarity. By aggregating temporally and spatially varying responses over the monitoring period and monitoring sites, respectively, we could assess the relative imprints of climate, land cover and random processes as drivers of community dissimilarity across birds, butterflies, and moths. According to the non-stationary models, we found a general imprint of environmental filtering on spatial dissimilarity with climate as the main environmental component. Our results were more mixed regarding temporal dissimilarity for which the average imprints of environmental filtering and random processes varied among species groups and were highly uncertain. Temporal dissimilarity was driven by a mix of climate and land cover with major variation between species groups (Fig. 3). On top of these general patterns, we found non-stationarities in spatial and temporal assembly processes and environmental associations, though clearly larger between-monitoring sites variance in the drivers of temporal dissimilarity. When combined, variability in the drivers of temporal

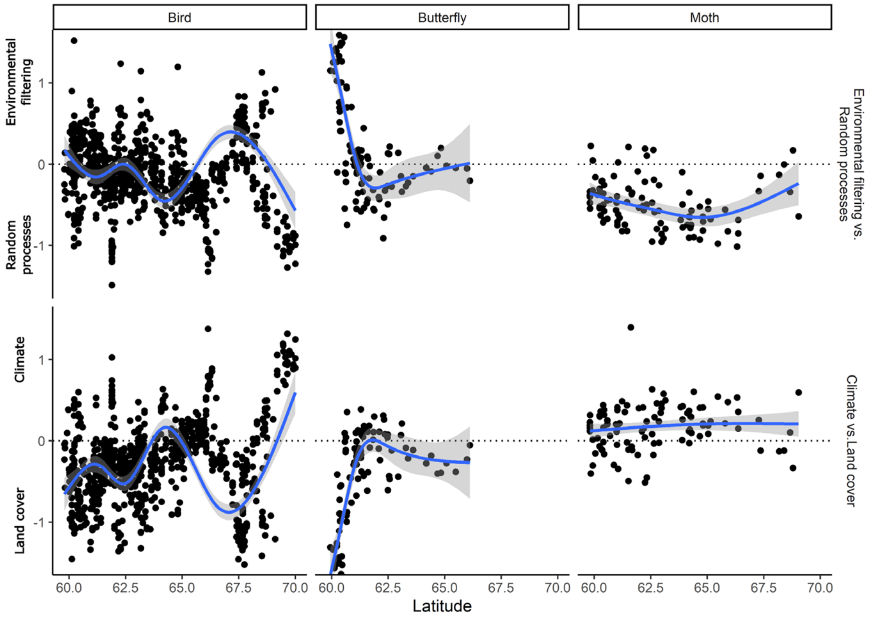

Figure 5. Latitudinal change in the imprint of environmental filtering versus random processes (top row) and climate versus land cover (bottom row). Dots denote monitoring sites, and the line denotes the spline-type mean over the sites in relation to latitude. Shaded areas denote the 95% credibility intervals. All species groups follow a different (though all non-linear) pattern along latitude in both of the comparisons: birds follow a complex function; butterflies follow a step-function, where the imprint of environmental filtering and land cover decline until 61°N after which the change stagnates; the average response of moths does not change along latitude.

dissimilarity between monitoring sites generated distinct latitudinal trends among species groups. Below, we will address each finding in turn.

Non-stationary drivers of spatial dissimilarity

Across species groups, we found a general imprint of climate-associated environmental filtering on spatial dissimilarity. The large imprint of climate-related environmental filtering can be explained by the relatively steep climatic gradient across Finland, a country that spans 11° of latitude and 1200 km in a North–South direction. Within this domain, strong climatic sorting has previously been found for butterflies and moths (Luoto et al. 2006, Pöyry et al. 2011). In contrast to these earlier reports, we did not find support for the purely climatic filtering of moth communities. However, non-stationary responses revealed a growing imprint of climate for butterflies and moths. These shifts are likely caused by climatically driven range expansions of southern species northwards (Antão et al. 2020, Hällfors et al. 2021). This would likely create stronger South–North directed stratification in the community composition so that generalist species, which tolerate different climatic conditions are replaced by warm-affiliated species in southern Finland. This community change would eventually result in a regime shift in the drivers of community dynamics.

Non-stationary drivers of temporal dissimilarity

In terms of temporal dissimilarity, we found large spatial variance in the imprints of environmental filtering versus random processes on especially birds and butterflies. This was at least partly due to the varying imprints of climate versus land cover on them. Interestingly, the difference in the

Table 1. Models fitted to evaluate the spatio-temporal dimensions of community dissimilarity. For each model, we define the study setup (spatio-temporal, spatial or temporal), the type of response (whether the imprints are assumed to be stationary or non-stationary in space or time), and the equation showing the model structure (with reference to the numbering of equations in the main text). By 'non-stationary', we refer to a type of model where the response between community turnover and explanatory variable may change between years or monitoring sites. Lastly, we include measure of model fit defined as the negative expected log posterior predictive density (−E[LPPD]). For non-stationary models (3 and 5), −E[LPPD] is shown in comparison to the respective stationary model. A smaller −E[LPPD] indicates a larger support for the model by the data.

					−E[LPPD]	
Model	Setup	Response	Equation	Bird	Butterfly	Moth
1	Spatio-temporal	Stationary	2	1.215	1.247	1.194
2	Spatial	Stationary	2	1.206	1.252	1.159
3	Spatial	Non-stationary	4	−0.056	−0.004	−0.012
4	Temporal	Stationary	2	1.105	1.232	1.131
5	Temporal	Non-stationary	5	−0.047	−0.019	−0.02

average estimates from models assuming stationary versus non-stationary responses were large enough to result in completely different conclusions for birds and butterflies. Models assuming stationary responses would lead us to conclude that climate is more important than land cover – whereas models assuming non-stationary responses will lead us to conclude the opposite. Accounting for the non-stationary responses for temporal dissimilarity showed that the declines in habitats, here mixed forests for birds and agricultural landscapes for butterflies, can act as major drivers of temporal community change (Supporting information). These findings are partly in line with earlier studies revealing a high importance of land cover for each of the species groups (Baselga et al. 2015 for birds; Kuussaari et al. 2007, Gossner et al. 2016 for insects; Merckx et al. 2019 for moths specifically). Other studies suggest interactive effects of climate and land cover over different habitat types (Jarzyna et al. 2015, Nieto-Sánchez et al. 2015, Jarzyna et al. 2016). Especially for birds, intense forestry may have created the strong effect of land cover-related filtering in southern and northeastern Finland (Korhonen et al. 2021). For a reason likely related to sampling design (discussed in a later section), stationary models did not bring out the imprints of land cover. In addition to external drivers, there can also be imprints of different community dynamics. Such effects may arise through more severe competition (i.e. large imprint of random processes) in southern sites, where species are immersed in larger species pool than at northern sites (Soininen et al. 2007, Qian et al. 2008). However, our results did not support such competition hypothesis as we did not find a linear decline in the relative imprint of random processes along the latitudinal gradient for temporal dissimilarity of any species group.

Generally, the conflicting results between stationary and non-stationary models show that community analysis is sensitive to the spatial scale for which community assembly processes are inferred. Conducting a study across a long climatic gradient and a diverse set of different land cover types without accounting for non-stationarities may then hide a suite of different community assembly processes at a local scale.

General support for non-stationary responses

Just why we may expect non-stationary responses in real landscapes is evident: monitoring sites have undergone different levels of land cover and climate changes (temporal dissimilarity) and annually varying weather conditions (spatial dissimilarity). We may also detect changes which are more consistent by their nature and could be labeled as regime shifts. It is only intuitive that communities experiencing different levels of habitat modification in space and time will show different imprints of environmental change. Nonetheless, most studies to date have effectively smudged this variation by quantifying a single imprint of environmental change across space and time or over multiple highly different monitoring sites and time periods. Overall, non-stationary responses could address sampling related issues, such as imbalanced sampling in relation to land cover modifications, and track community dynamics in a higher level of detail than stationary models were able to.

The importance of addressing non-stationary responses was shown by an improvement in the model performance (−E[LPPD]) for non-stationary models as compared to stationary models assuming stationary responses (Table 1). Thus, we find that our approach offers a transparent and clear-cut approach to account for ubiquitous variation in natural settings.

In evaluating our current findings, we note that the effects of land cover can be sensitive to the choice of buffer size around monitoring sites. Although we did use different buffer sizes for species groups (to thereby account for their different dispersal abilities), the buffers chosen may still not match the exact geographical range utilized by the species. This may reduce the model precision, as it will cause random deviations between the land cover types inside the buffer and the land cover types accessible to a species. However, it should not create systematic bias, as monitoring sites are randomly placed in the landscape. Another source of error is the differing spatial resolution and monitoring frequency of climate (10 km; daily) versus land cover (30 meter; six years). Although coarser spatial resolution should reduce the effect size for climate, we still found a detectable imprint of climate variables in our analyses. We found that during the monitoring periods, climatic conditions have become warmer and wetter, whereas changes in land use have been more variable (Supporting information). Hence, we believe that despite the varying covariate resolution and buffer size, we could still capture the direction and magnitude of climate and habitat changes.

Estimating community assembly processes from long-term monitoring data

We argue that standard approaches to modeling spatio-temporal community dissimilarity may serve to obfuscate disparate and even conflicting processes. We found seemingly conflicting results regarding the importance of environmental filtering and random processes for spatial and temporal dissimilarity. Importantly, the conflict was consistent between stationary and non-stationary models. Here, we should note that estimates of environmental imprints on spatio-temporal community dissimilarity are sensitive to the study design, and to the balance between spatial and temporal replicates of the data. This consideration has been previously brought up by Magurran et al. (2010) and Guzman et al. (2022). In vivid illustration of it, any spatio-temporal analysis built on only a few replicates in time over multiple sites in space is bound to reflect mostly spatial community dissimilarity. Here we found that the spatio-temporal model did not reflect well non-stationary models for either spatial or temporal dissimilarity. A spatio-temporal model assuming stationary effects may then poorly represent the true forces structuring local communities.

Just as spatio-temporal models will be sensitive to the study design, spatial and temporal models with stationary responses are also sensitive to imbalanced sampling. The discrepancies detected in the current study can be attributed to the fact that for the stationary model, we computed effects over pairwise comparisons, whereas for the non-stationary models, we computed effects over groups of pair-wise comparisons. The average effect of stationary models will then overrepresent those years and sites from which we have relatively more samples. Our results show that non-stationary responses can address imbalanced sampling strategies, yielding reliable estimates of community-level responses over areas or time periods. For birds and butterflies, stationary models represented monitoring sites which are relatively intact have relatively longer sampling histories and deflate the impact of the sites which have undergone a more serious land cover change. Non-stationary responses could account for the imbalance in the site-level monitoring periods and return spatially more representative estimates for the drivers of the community change. Moreover, the explicit quantification of uncertainty in spatially non-stationary responses for temporal dissimilarity may guide us in refining the study design. For example, high uncertainty in the average imprints related to birds' and butterflies' temporal dissimilarity originated from large spatial variance highlighting the importance of non-stationary approaches.

Conclusions

Overall, we argue that resolving variability of responses is essential to answer theoretical and applied questions about how communities change.

First, non-stationary responses connect community data to scaling rules of ecological processes. For spatial and temporal dissimilarity, we found inconsistent scaling in time and space, respectively, as reflected by varying responses between years and between monitoring sites.

Second, non-stationary responses explain locally varying diversity patterns. Earlier studies have shown diverse temporal trends of beta-diversity (Dornelas et al. 2014, Blowes et al. 2022), but have failed to reveal any explicit associations between assembly processes and environmental change. In our study, we were able to attribute patterns of community dissimilarity across species groups to plausible patterns in the state of the drivers. We believe that non-stationary responses can explain a suite of diversity patterns with the ecological scaling of underlying processes.

Third, comparing the effects of climate and land cover as drivers of community dissimilarity across localities allows us to study the sensitivity of communities to extrinsic pressures (Jaureguiberry et al. 2022). In this context, we were able to pinpoint regions where community dissimilarity was disproportionately affected by changes in land cover. For birds, these regions occur in areas which are characterized by recent changes in forest cover and agricultural areas (Supporting information).

By testing the importance of different assembly processes in a large spatio-temporal context, our study responds to the call of McGill and Algar (2018) for linking metacommunity theory to macroecology and global change ecology. Our approach provides a key extension to the methodological toolbox for studying community-level responses to environmental change over diverse habitats and reveals how these variable imprints are brought out in practice, across a full nation and across multiple organism groups. Most importantly, non-stationary assembly processes provide us with a concept for analyzing biome-wide community dissimilarity as a sum of simultaneously operating drivers.

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Author contributions

Jussi Mäkinen: Conceptualization (equal); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Laura Antão**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Janne Heliölä**: Data curation (equal); Writing – review and editing (supporting). **Mikko Kuussaari**: Data curation (equal); Writing – review and editing (supporting). **Aleksi Lehikoinen**: Data curation (equal); Writing – review and editing (supporting). **Ida-Maria Huikkonen**: Data curation (equal); Writing – review and editing (supporting). **Reima Leinonen**: Data curation (equal); Writing – review and editing (supporting). **Juha Pöyry**: Data curation (equal); Writing – review and editing (supporting). **Tomas Roslin**: Conceptualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.07335.

Data availability statement

The original monitoring data sets are openly available for moths (https://laji.fi/en/observation/list?collectionId=HR.4511) and birds (https://laji.fi/observation/list?target=MX.37580&collectionId=HR.61). For butterflies, the data are not directly available as the data users need to commit to the user policies of the eBMS network. However, the data are accessible as part of a wider European butterfly transect dataset through eBMS after formally completing a license form (https://butterfly-monitoring.net/ebms-data%20access).

The aggregated community turnover and environmental dissimilarity data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.905qfttsh (Mäkinen et al. 2025).

Supporting information

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

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