

A niche-based approach for evaluating the mechanisms of community stability in butterflies

Luke Evans¹, Yolanda Melero², Reto Schmucki³, Philipp Boersch-Supan⁴, Lluís Brotons⁵, Colin Fontaine⁶, Frederic Jiguet⁷, Mikko Kuussaari⁸, Dario Massimino⁴, Robert Robinson⁴, David Roy⁹, Oliver Schweiger¹⁰, Josef Settele¹¹, Constanti Stefanescu¹², Chris van Turnhout¹³, and Tom Oliver¹

¹University of Reading

²CREAF

³UK Centre for Ecology & Hydrology

⁴BTO

⁵Centre de Recerca Ecològica i Aplicacions Forestals (CREAF)

⁶Museum National d'Histoire Naturelle

⁷Centre d'Ecologie et de Sciences de la Conservation

⁸Finnish Environment Institute

⁹Centre for Ecology & Hydrology

¹⁰Helmholtz Centre for Environmental Research - UFZ

¹¹UFZ - Helmholtz Centre for Environmental Research

¹²Universitat Autònoma de Barcelona Centre de Recerca Ecològica i Aplicacions Forestals

¹³SOVON Dutch Centre for Field Ornithology

April 05, 2024

Abstract

Species niches may impact population and community stability by influencing average population sizes and species richness, however, niche-based approaches are rarely applied when studying stability in natural communities. Here we utilise a niche-based approach to link niche characteristics to community stability in 140 European butterfly communities. We represent niches as hyper-volumes and generate metrics for niche overlap, mismatch, and volume. Using structural equation modelling we then test five hypotheses linking niche and community characteristics to mechanisms influencing community stability. We find that the position of a site relative to the niches of the species pool predicts species richness, and that sites with species near the centre of their niche have higher mean abundance. We then show that niche position and size influence population stability, and species richness increases asynchrony which subsequently influences community stability. Our approach demonstrates that niches metrics are useful tools for understanding the dynamics of natural communities.

Introduction

The factors affecting community stability are important to understand as community stability ultimately underpins the stability of ecosystem function (Millennium Ecosystem Assessment 2005; Cardinale *et al.* 2012). A central problem is how species diversity (richness) contributes to stability (Elton 1958; May 1972; Tilman & Downing 1994; Tilman 1999). Community stability is influenced by two properties of the community: average population stability and asynchrony (Doak *et al.* 1998; Tilman *et al.* 1998; Yachi & Loreau 1999; Thibaut & Connolly 2013). Briefly, average population stability describes the variability of each population

over time and can be influenced by factors such as mean-variance scaling, where larger populations are relatively less variable (Taylor 1961; Kilpatrick & Ives 2003) as well as density-dependent (e.g. pathogen-induced mortality) and density-independent processes (e.g. mortality induced by extreme weather events). Population asynchrony constitutes negatively correlated population dynamics, which can be driven by species interactions (e.g. competition) or through varying responses to environmental conditions. Average asynchrony between the populations in a given community is expected to increase with species richness (Thibaut & Connolly 2013), but associations between richness and average population stability are less obvious (Jiang & Pu 2009).

Though the theoretical background of community stability is well developed, the mechanisms have not been tested in natural animal communities and much experimentation has been conducted with plant or aquatic communities (Diaz & Cabido 2001; Craven *et al.* 2018; van der Plas 2019). For example, asynchrony increases with species richness in grassland communities (Roscher *et al.* 2011; Isbell *et al.* 2019), but less is known about how richness impacts asynchrony or its importance in animal communities. Previous work suggests that the relative importance of the mechanisms can vary between taxa, with some studies finding a prominent role for asynchrony in driving community stability (Jucker *et al.* 2014; Ma *et al.* 2017). For example, asynchrony is observed as key to the stability of arthropod and plant communities between different habitat types (Blüthgen *et al.* 2016), while work on intertidal and algal communities suggest average population stability can explain differences in community stability (Pennekamp *et al.* 2018; White *et al.* 2020).

To understand why the impact of these mechanisms varies between communities, it is important to quantify both how asynchrony or population stability contribute to community stability and also the factors leading to differences in synchrony and stability. Three main forces influence correlations among the dynamic of species populations: intra- and inter-specific interactions, differing responses to environmental variations, and demographic stochasticity (Roscher *et al.* 2011). A key factor for insect communities is the response to environmental fluctuations (Ives *et al.* 1999). The distributions of butterflies are strongly influenced by climate (Settele *et al.* 2008) and population dynamics by weather (WallisDeVries *et al.* 2011; Palmer *et al.* 2017). Consequently, responses to environmental variation could be important in understanding differences in stability. However, a challenge when linking weather to synchrony in natural communities is that the importance of environmental variables will vary among species (Roy *et al.* 2001; WallisDeVries *et al.* 2011; McDermott Long *et al.* 2017).

Additionally, at local scales species richness and abundance may vary due to the suitability of sites, or at large scales, due factors such as latitudinal gradients in richness (Hillebrand 2004). For example, the abundant centre hypothesis posits that species will be most abundant at locations near the centre of their range (Andrewartha & Birch 1954; Brown 1984; Lawton 1993), and so sites located near many species' range centres should have higher population stability due to mean-variance effects (i.e. larger populations being relatively less variable over time) (Oliver *et al.* 2012, 2014). The importance of asynchrony or population stability may then vary due to community structure, e.g. differing levels of interspecific competition (Lehman & Tilman 2000). Finally, varying sensitivities to environmental variation (Ives *et al.* 1999) may then drive differences in population variability and contribute to the degree of asynchrony in a community.

To tackle this complexity, we apply the ecological niche concept, i.e. a species tolerance to different environmental variables, can be represented as an n-dimensional space (Hutchinson 1957). Fundamental to niche modelling, at both the species and community scales (Hirzel & Le Lay 2008; Poggiato *et al.* 2021), is that species occurrence under local conditions is dictated predominantly by the niche space. Consequently, notwithstanding nuances of extinction debt and colonisation credit (Tilman *et al.* 1994; Kuussaari *et al.* 2009), species richness should be predictable from the location of a site relative to the niches of the species in the regional species pool. Similarly, mean abundance should be informed by site position relative to the niches of the species at the site (Osorio-Olvera *et al.* 2020). Species at the edge of their niche may also have lower average population stability (Oliver *et al.* 2012; Mills *et al.* 2017) and species with larger niche breadths may be more robust to local environmental variation. Finally, when a site is in a different niche position for two species, they may have differing responses to environmental variation at the site – generating asynchrony.

We apply the niche-based approach to study 140 butterfly communities spanning a European scale from Finland to Northeast Spain. We utilise a computationally fast approach to generate bioclimatic niche hypervolumes (Blonder *et al.* 2014, 2018) for each species. We then derive niche-based metrics to test potential factors affecting first species richness, mean abundance, and then the mechanisms of community stability. Specifically, we test five expected responses associated with key mechanisms: 1) species richness will be higher if the site is located at shorter distances to the niche centres of the total species pool; 2) mean abundance will be greater when the site is nearer to the niche centres of the species at the site; 3) average asynchrony between pairs of species in a community will be greater if the niches of species are more dissimilar at a site, and will also increase with species richness; 4) average population stability will be highest when the site is nearer the centre of the species niches, when the average niche breadth of species is larger (i.e. more resilient to local weather anomalies), and when the average abundance of the species is greater; 5) asynchrony and average population stability will explain differences in community stability.

Materials and methods

Butterfly data

Data were collected with Butterfly Monitoring Schemes running in Finland, Northern Spain (Catalonia), and the UK. In these schemes, volunteers count butterflies along line transects following a standardised framework called the 'Pollard walk' (Pollard & Yates 1993). The counts are then processed using generalized additive models (GAMs) to give an index of abundance per site and per year (Dennis *et al.* 2013; Schmucki *et al.* 2016). Note that a single number is provided both for multivoltine and univoltine species, therefore it is the total abundance across the observation period. If there are missing counts at a site, the GAM model interpolates abundance based on counts made at other sites in the same bioclimatic zone (Metzger *et al.* 2013), producing unbiased estimates of abundance (Schmucki *et al.* 2016).

In the different countries, the number of sites and the duration of monitoring varies: Finland (1999, number of sites = 107), Spain (1994, n = 130) and the U.K. (1976, n = 2128). Therefore, the country with the scheme of shortest duration, Finland, set the time period for our study (1999-2017), and only sites with ≥ 10 years of data were retained, leaving 59 and 55 sites from Spain and Finland respectively. To maintain a balance in the sampling between the countries, 60 sites with ≥ 10 years of data were randomly sampled from the larger collection of UK sites under a condition that each was >20 km from the others. To assure robust estimates from the GAM, indices of abundance with $>50\%$ of missing observations were also removed. This retained the same number of transect sites (n=174) but removed some years at sites when the counts were made infrequently. A further 31 sites were removed prior to the final analysis, as they either contained only one species (n=3), there was an insufficient overlap of species occurrences to calculate asynchrony, or too few occurrences per species to calculate average population stability (n=28); note this occurred after species were removed due to data limitations when constructing the hypervolume (below). This left a final dataset of 143 sites.

Niche construction

To construct the bioclimatic niche hypervolumes for each species we first extracted observations from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/ipt/>) over a 30 year period (1970-2000) using the 'rgbif' R package (Chamberlain *et al.* 2020) using the R statistical software (R Core Development Team 2019).

We next utilised 19 'bioclimatic' variables provided by WorldClim 2.1 (Fick & Hijmans 2017) at a resolution of 2.5 arc minutes and clipped the data to the approximate region of the species observations (i.e. western Europe; Figure 1). WorldClim's bioclimatic variables are derived from temperature and precipitation records and represent both mean and extreme conditions at a location. We fitted a PCA to the bioclimatic variables. The first six axes were retained as they represented $>95\%$ of the variance across the 19 bioclimatic variables. For each species observations, we collected the first six coordinates projected onto this PCA space and used this to fit a 6-D hypervolume using multidimensional kernel density estimation (Blonder *et al.* 2014) using the hypervolume package (Blonder *et al.* 2014, 2018). Twelve species were removed from all further

analyses at this point as there was an insufficient number of observations to fit the hypervolume algorithm; thus we retained data for 145 species in total. The removed species, being very rare, have little impact on community properties. We also removed data on populations where species occurred at sites only very infrequently (zero counts for >25% of years) as these provide unreliable estimates of population stability and may bias community niche metrics (below).

Niche and community metrics

The analysis required the calculation of four niche-based metrics and three measures associated with stability. For clarity, we provide again the hypotheses and then describe the associated metrics. Starting with hypothesis one, species richness is predicted to increase if a site is located nearer to the centre of the niches of more of the total species pool (i.e. all 145 species). Species richness was the number of species observed at the monitoring site during the study period. To construct the average distance between the site location in niche space and the species pool niche centres, we took the average of the Euclidean distance between the site's location in 6D and the niche centroid of every species, hereafter referred to as overall niche distance. Thus a site with a larger overall niche distance is further away from the niche centre of the total species pool.

Hypothesis two predicts that mean abundance will increase as species are nearer the centre of their fundamental niche. Therefore we calculated a mean abundance across all species for each site – density was used to account for differences in transect length between study sites. To calculate the distance of species to their niche centres, we took the weighted average Euclidean distance between the niche centroids of each species found at a site and the location of the site in 6D. The weighting means that the distance of the most abundant species in a community is weighted most highly. This was applied so that niche distances account for differences in evenness across communities. We term this measure niche-mismatch as we refer to it repeatedly in the analysis.

Hypothesis three states that asynchrony will increase with species richness and if species have lower niche-overlap. To measure asynchrony (synchrony) at a site we follow the summary measure detailed in Thibaut and Connolly (2013):

$$\text{Synchrony} = \frac{\sum_{ij} V(i,j)}{(\sum_i \sqrt{V(i,i)})^2}$$

Here i and j refer to species at a site, the numerator is the sum of all elements of the covariance matrix of the species at a site, and the denominator is the species level variances in the presence of perfect synchrony. This measure is therefore standardised, accounting for differences in richness and variance. The synchrony index always takes a score between 0 – no synchrony or population variance, and 1 – perfect synchrony. To measure niche-overlap we utilised Jaccard Similarity which is the intersection of a pair of species niches divided by their union, once again always scoring between 0 and 1. This was calculated for all pairwise comparisons (Blonder et al., 2015) and the mean was used to give an overall niche-overlap score.

Hypothesis four states that average population stability will be highest when the site is nearer the centre of the species niches, when the niche breadth of species is larger, and when the abundance of the species is higher. To calculate average population stability, we again follow Thibaut and Connolly (2013):

$$\text{Average population stability} = \sum_i \frac{m(i)}{mc} \frac{m(i)}{\sqrt{V(i,i)}}$$

Here $m(i)$ refers to the mean abundance of species i and mc refer to the sum of species mean abundances in the community, thus the score is abundance weighted. The second term is the mean of the species abundance divided by the standard deviation – the inverse coefficient of variation (Tilman 1999). For distance to the centre of the niche, we utilised niche mismatch as calculated above. For niche breadth, we took the abundance-weighted mean volume of the niches at the site.

Hypothesis five predicts that asynchrony and average population stability will explain differences in community stability. For community stability, we again utilised the inverse coefficient of variation.

$$(3) \text{ Community stability} = \frac{\mu}{\sqrt{V(i,i)}}$$

Where μ refers to mean abundance for all species at the site.

Structural equation model

As the same metrics are used in multiple hypotheses, we utilised a piecewise structural equation modelling approach. The 'base' model was constructed through linear models developed from the relationships assumed in hypotheses 1-5 (Figure 2). Mean abundance was log-transformed to meet the assumptions of the linear model. We noted relationships with species richness $\rightarrow$ synchrony, and synchrony $\rightarrow$ community stability were non-linear, a quadratic term included in these models was significant but produced an overall model with a higher AIC and with qualitatively similar results for all other relationships. Therefore, we retain the simpler model with all relationships modelled as linear. For the models predicting species richness and abundance, it was necessary to account for other unmeasured biogeographic differences between the countries (Settele *et al.* 2008). As categorical variables are challenging to interpret in a structural equation approach, we modelled unmeasured spatial correlation using Generalized Least Squares (GLS) with an exponential spatial correlation structure.

In addition to the base model, we included some additional correlated errors between observed variables not accounted for in the main models. Initially, we included a dependency between mean abundance and species richness due to possible differences in site quality, as it may be that high-quality sites are more species-rich and abundant than expected given climatic niche position. However, this was not significant correlation and was removed for parsimony. Tests of directed separation were then used to assess dependencies in the model (Shipley 2000). This identified five missing dependencies in the model, three of these were added as paths as they predicted one of the response variables in the model (mean niche volume $\rightarrow$ species richness, mean niche volume $\rightarrow$ log mean abundance, niche overlap $\rightarrow$ log mean abundance). However, the other two relationships were fitted with correlated errors as they were not dependent variables, and were likely a statistical consequence of increases in species richness; these were that increased species richness predicted lower niche-overlap and greater niche-mismatch.

The piecewise structural model analysis was conducted using the piecewiseSEM R package (Lefcheck 2016) and the GLS was fitted using nlme (Pinheiro *et al.* 2019). All analyses were conducted in R 3.6.1 (R Core Development Team, 2019).

Results

Results for all hypotheses are summarised in Figures 2 and 3, and Table 1. Fischer's C, a measurement of conditional independence was 29.23 ($p = 0.4$, $df = 28$) for the structural equation model, suggesting no missing dependencies in the model. For hypothesis one, increases in overall niche distance reduced species richness, and a path was added from mean niche volume to species richness, finding greater niche volumes were associated with greater species richness. Therefore, species richness decreased with the average distance of a site in niche-space to the average of the total species pool supporting hypothesis one (Figure 2; Figure 3a; Table 1), and more species-rich sites contained species with higher niche volume on average.

Our second hypothesis was that mean abundance will be greater when the site is nearer to niche centres of the species at the site. This was supported as we found log mean abundance decreased with niche mismatch so that species nearer the centre of their range were, on average, more abundant (Figure 2; Figure 3b; Table 1). Log mean abundance also increased with mean niche volume and an additional path was added showing increasing niche overlap was associated with increasing log mean abundance – we discuss possible reasons for this below.

Our third hypothesis was that synchrony will be reduced if the niches of the species were more dissimilar. This was less well supported as species richness decreased synchrony (increased asynchrony), but niche overlap had no significant effect (Figure 2; Figure 3d; Table 1). We also found a relationship between species richness and niche overlap, with overlap decreasing with higher species richness, indicating that richer communities

were composed of species with more dissimilar niches.

Our fourth hypothesis was that average population stability would be greater when the site was nearer the centre of the species niches and when the niche breadth of species was larger. This was partly supported as niche mismatch decreased average population stability, but, contrary to expectation, increased mean niche volume decreased average population stability, and mean population abundance had no significant effect (Figure 2; Figure 3c; Table 1). There was also no significant effect of log abundance on population stability.

Finally we hypothesised synchrony and average population stability will explain differences in community stability. Synchrony reduced community stability while average species stability increased community stability (Figure 2; Figure 3e,f; Table 1). After accounting for these effects, species richness and log mean abundance also increased community stability.

Discussion

We utilised a niche-based approach to investigate five hypotheses relating to factors influencing community stability. Our first hypothesis supported was that species richness will be higher if the site was located closer to the niche centre of the species pool. This was expected as niche-distribution modelling is dependent on the relationship between species niche-space and the probability of occurrence (Elith & Leathwick 2009). We add here that a simple aggregate score was informative about the species richness of our communities. This, however, leaves room for improvement when predicting niche effects on richness, such as utilising individual niche models to sum occurrence at each site, or alternatively, applying joint approaches that utilise species covariances to improve predictive performance (Poggiato *et al.* 2021). A spatial correlation structure also accounted for differences in species richness not accounted for by climatic niche characteristics. Other factors are, therefore, important for predicting richness such as latitudinal gradients in species richness (Hillebrand 2004), lower species richness of island faunas (MacArthur & Wilson 1967), and with smaller scale effects such as changing land cover.

That our second hypothesis was supported, lends the first large scale support for the abundant centre hypothesis (Andrewartha & Birch, 1954; Brown, 1984; Lawton, 1993) operating in butterfly communities. The effect size here was modest, however, we applied a simple aggregate metric (mean niche mismatch) and more variation in abundance might be explained for each species by niche mismatch. Similarly, increasing the dimensionality of our niche constructions, or accounting for other factors such as land use may better isolate the effect of niche position on abundance. We also found increased niche volume was associated with increased mean abundance. This suggests that in communities where species had larger niches, i.e. more generalist in terms of climate association, the populations were larger. This could be a reflection of the wide-scale declines that have been noted for specialist species (Clavel *et al.* 2011). However, studies of generalist-specialist trends in butterflies typically utilise species traits, including host plant association, and focus on single countries (Stefanescu *et al.* 2011; Dapporto & Dennis 2013; Eskildsen *et al.* 2015) and so linking these results must be cautious. Nevertheless, our results suggest that evaluating species trends in relation to climatic niches could be valuable, particularly given the recent, and projected, increase in extreme climatic events (Donohue *et al.* 2016; Ummenhofer & Meehl 2017). Finally, a path not predicted a priori, suggested communities with higher niche overlap had populations that were on average more abundant. It is possible, that after accounting for niche mismatch, a community with greater overlap means more species situated in optimal conditions producing a positive association between high overlap and abundance. However, we suggest further work is needed to resolve interactions between niche overlap, volume, and mismatch.

Results from our third hypothesis showed a significant negative association between species richness and synchrony, thereby supporting a key diversity-stability mechanism for butterfly communities (Thibaut & Connolly, 2013). That we found no effect of climatic niche-overlap on synchrony is surprising as butterflies are strongly influenced by weather (McDermott Long *et al.* 2017). This suggests that other factors, such as species traits and local adaptation, may also be needed to predict species responses to weather variation. Alternatively, the niches constructed here using yearly average weather apply space-for-time substitutions

that might be too coarse to account for the weather events causing changes in population size (White & Kerr 2006). Our results suggest that other factors must generate asynchrony. One factor could be intra-specific density dependence of population growth rates (Roy *et al.* 2001) as density varies between species, asynchrony could occur even between species with similar climatic niches. We also noted additional associations, as niche overlap decreased and niche mismatch increased with species richness. The relationship with niche-overlap is perhaps expected as, so long as the niche shapes vary between species, then adding species will reduce overlap. The result with niche mismatch is harder to interpret, but could be due to sites with higher species richness include more species near the edges of the niche positions, or that the UK with a moderate climate and lower species richness may induce a niche-mismatch and species richness association.

Results from our fourth hypothesis were partly as predicted. Average population stability decreasing with niche mismatch is an extension of the abundant centre hypothesis, and natural populations at range edges have previously been shown to be more variable (Oliver *et al.* 2012; Mills *et al.* 2017). However, we expected mean niche volume to increase average population stability as species with broader niches should tolerate a wider range of conditions leading to higher stability. It is possible that species with broader niches tolerate more marginal conditions leading to lower stability at a site while still being able to persist. Species with broad niches may also be more affected by competition, reducing the stability of the population. By comparison, specialists with narrower niches may only occupy favourable areas where they are generally more stable and relatively freer from inter-specific competition. Finally, we found no effect of mean abundance on average stability which is surprising due to expected mean-variance relationships (Taylor 1961; Kilpatrick & Ives 2003). However, mean abundances take no account of species weighting, whereas species stability was abundance weighted so that the evenness of the community might obscuring the effect.

Finally, we hypothesised synchrony and average population stability will explain differences in community stability (Doak *et al.* 1998; Tilman *et al.* 1998; Thibaut & Connolly 2013; Wang & Loreau 2014) was supported. The standardised effect size (Table 1) and the model fits (Figure 3e,f) suggest that asynchrony was, overall, having a larger impact on community stability as expected from theoretical considerations (Thibaut & Connolly 2013; Wang & Loreau 2014). In butterfly communities asynchrony may be particularly important as being r-selected – with high reproductive and interannual population growth rates – populations are characterised by high levels of population variability (Pianka 1970; May 1974), and community stability may be more influenced by how the dynamics of populations combine than differences in population stability. Mean abundance also increased community stability. This is expected from mean-variance scaling relationships, such as Taylor’s power law (Taylor 1961; Kilpatrick & Ives 2003) and we show this affects the stability of butterfly communities in the aggregate even if it was not detected at the individual level. In addition to asynchrony, we also noted that species richness increased stability through mechanisms not directly accounted for. This could be related to how species richness reflects the evenness of species. For example, if species-poor communities are dominated by one species in terms of absolute abundance, then even with high levels of asynchrony, the aggregate community abundance will largely reflect the population variability of the dominant species (Grime 1998).

Our approach demonstrates that consideration of hyper-dimensional niches and the derived metrics are useful for understanding population and community dynamics (Barros *et al.* 2016). To date, they have been applied more in plant communities (Enrique *et al.* 2018; Papuga *et al.* 2018), though their uses for predicting biogeography of populations has been recently demonstrated for birds (Osorio-Olvera *et al.* 2020). However, there are some possible weaknesses in our approach. First, several metrics can be generated from niche-hyper-volumes (Mammola 2019) and for some hypotheses different metrics may have been more effective. For example, niche mismatch could consider minimum distances from niche volumes to site locations, and Mahalanobis distances could provide better measures than Euclidean distances from the centroids. Similarly, niche-overlap could be quantified using a range of metrics. However, we justify our efforts here as applying a straightforward approach that uses a minimum number of intuitive metrics to test key hypotheses regarding butterfly community stability. A second limitation of the niche approach is that the strength of any one event on any single niche dimension is not measured as directly. Consequently, identifying the threats of any class of extreme event such as drought (Oliver *et al.* 2013; De Palma *et al.* 2017) may still require a

single variable approach. Combining the approaches, for example tolerance to drought would be predicted to have lower scores on an axis related to precipitation-aridity, could provide a way to test and generate new hypotheses around the factors affecting the population dynamics of species.

In conclusion, we find support for the mechanisms purported to influence community stability operating in butterfly communities. We utilised metrics derived by niche hyper-volumes to provide a unique overview of the environmental drivers behind these mechanisms. Thus, our method provides a novel test of factors affecting the stability of terrestrial animal communities and demonstrates how considering niches can allow consideration of mechanisms, operating at a range of scales, that ultimately influence community stability.

Acknowledgments

We thank the volunteers collecting butterfly data and the funders of the schemes for the obtaining the data required for this study. The UK Butterfly Monitoring Scheme is organized and funded by Butterfly Conservation, the Centre for Ecology and Hydrology, British Trust for Ornithology, and the Joint Nature Conservation Committee. The Catalan BMS is funded by the Catalan Government, the Barcelona Provincial Council and other local partners. The Catalan BMS also incorporates the Andorra BMS that is run by CENMA and funded by Govern d'Andorra. The Finnish BMS is organized and funded by the Finnish Environment Institute (SYKE) and the Finnish Ministry of Environment.

References

- Andrewartha, H.G. & Birch, L.C. (1954). *The distribution and abundance of animals*. University of Chicago press.
- Barros, C., Thuiller, W., Georges, D., Boulangeat, I. & Münkemüller, T. (2016). N- dimensional hypervolumes to study stability of complex ecosystems. *Ecology Letters* , 19, 729–742.
- Blonder, B., Lamanna, C., Violle, C. & Enquist, B.J. (2014). The n -dimensional hypervolume. *Global Ecology and Biogeography* , 23, 595–609.
- Blonder, B., Morrow, C.B., Maitner, B., Harris, D.J., Lamanna, C., Violle, C., *et al.* (2018). New approaches for delineating n -dimensional hypervolumes. *Methods in Ecology and Evolution* , 9, 305–319.
- Bluthgen, N., Simons, N.K., Jung, K., Prati, D., Renner, S.C., Boch, S., *et al.* (2016). Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nature Communications* , 7, 10697–10697.
- Brown, J.H. (1984). On the Relationship between Abundance and Distribution of Species. *The American Naturalist* , 124, 255–279.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature* , 486, 59–67.
- Chamberlain, S., Barve, V., Mcglinn, D., Oldoni, D., Desmet, P., Geffert, L., *et al.* (2020). *rgbif: Interface to the Global Biodiversity Information Facility* .
- Clavel, J., Julliard, R. & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* , 9, 222–228.
- Craven, D., Eisenhauer, N., Pearse, W.D., Hautier, Y., Isbell, F., Roscher, C., *et al.* (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology and Evolution* , 2, 1579–1587.
- Dapporto, L. & Dennis, R.L.H. (2013). The generalist–specialist continuum: Testing predictions for distribution and trends in British butterflies. *Biological Conservation* , 157, 229–236.
- De Palma, A., Dennis, R.L.H., Brereton, T., Leather, S.R. & Oliver, T.H. (2017). Large reorganizations in butterfly communities during an extreme weather event. *Ecography* , 40, 577–585.

- Dennis, E.B., Freeman, S.N., Brereton, T. & Roy, D.B. (2013). Indexing butterfly abundance whilst accounting for missing counts and variability in seasonal pattern. *Methods in Ecology and Evolution* , 4, 637–645.
- Diaz, S. & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* , 16, 646–655.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998). The Statistical Inevitability of Stability-Diversity Relationships in Community Ecology. *The American Naturalist* , 151, 264–276.
- Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., *et al.* (2016). Navigating the complexity of ecological stability. *Ecology Letters* , 19, 1172–1185.
- Elith, J. & Leathwick, J.R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual review of ecology, evolution, and systematics* , 40, 677–697.
- Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants* . Springer US, Boston, MA.
- Enrique, G., Violle, C., Perez-Ramos, I.M., Maranon, T., Navarro-Fernandez, C.M., Olmo, M., *et al.* (2018). A multidimensional functional trait approach reveals the imprint of environmental stress in Mediterranean woody communities. *Ecosystems* , 21, 248–262.
- Eskildsen, A., Carvalheiro, L.G., Kissling, W.D., Biesmeijer, J.C., Schweiger, O. & Hoyer, T.T. (2015). Ecological specialization matters: long-term trends in butterfly species richness and assemblage composition depend on multiple functional traits. *Diversity and Distributions* , 21, 792–802.
- Fick, S.E. & Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* , 37, 4302–4315.
- Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* , 86, 902–910.
- Hillebrand, H. (2004). On the Generality of the Latitudinal Diversity Gradient. *The American Naturalist* , 163, 192–211.
- Hirzel, A.H. & Le Lay, G. (2008). Habitat suitability modelling and niche theory. *Journal of Applied Ecology* , 45, 1372–1381.
- Hutchinson, G.E. (1957). Concluding remarks. *Cold spring harbor symposium on quantitative biology* , 22, 415–427.
- Isbell, F., Tilman, D., Reich, P.B. & Clark, A.T. (2019). Deficits of biodiversity and productivity linger a century after agricultural abandonment. *Nat Ecol Evol* , 3, 1533–1538.
- Ives, A.R., Gross, K. & Klug, J.L. (1999). Stability and Variability in Competitive Communities. *Science* , 286, 542–544.
- Jiang, L. & Pu, Z. (2009). Different Effects of Species Diversity on Temporal Stability in Single-Trophic and Multitrophic Communities. *The American Naturalist* , 174, 651–659.
- Jucker, T., Bouriaud, O., Avacaritei, D. & Coomes, D.A. (2014). Stabilizing effects of diversity on above-ground wood production in forest ecosystems: linking patterns and processes. *Ecology Letters* , 17, 1560–1569.
- Kilpatrick, A.M. & Ives, A.R. (2003). Species interactions can explain Taylor's power law for ecological time series. *Nature* , 422, 65–68.
- Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., *et al.* (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in ecology & evolution* , 24, 564–571.

- Lawton, J.H. (1993). Range, population abundance and conservation. *Trends in Ecology & Evolution* , 8, 409–413.
- Lefcheck, J.S. (2016). piecewiseSEM : Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution* , 7, 573–579.
- Lehman, C.L. & Tilman, D. (2000). Biodiversity, Stability, and Productivity in Competitive Communities. *The American Naturalist* , 156, 534–552.
- Ma, Z., Liu, H., Mi, Z., Zhang, Z., Wang, Y., Xu, W., *et al.* (2017). Climate warming reduces the temporal stability of plant community biomass production. *Nature Communications* , 8, 15378–15378.
- MacArthur, R.H. & Wilson, E.O. (1967). *The theory of island biogeography* . Princeton University Press, Princeton.
- Mammola, S. (2019). Assessing similarity of n- dimensional hypervolumes: Which metric to use? *Journal of Biogeography* , 46, 2012–2023.
- May, R.M. (1972). Will a large complex system be stable? *Nature* , 238, 413–414.
- May, R.M. (1974). Biological populations with non-overlapping generations: stable points, stable cycles and chaos, 186, 645–647.
- McDermott Long, O., Warren, R., Price, J., Brereton, T.M., Botham, M.S. & Franco, A.M.A. (2017). Sensitivity of UK butterflies to local climatic extremes: which life stages are most at risk? *Journal of Animal Ecology* , 86, 108–116.
- Metzger, M.J., Bunce, R.G.H., Jongman, R.H.G., Sayre, R., Trabucco, A. & Zomer, R. (2013). A high-resolution bioclimate map of the world: a unifying framework for global biodiversity research and monitoring. *Global Ecology and Biogeography* , 22, 630–638.
- Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: Synthesis* . Ecosystems . Island Press, Washington DC.
- Mills, S.C., Oliver, T.H., Bradbury, R.B., Gregory, R.D., Brereton, T., Kuhn, E., *et al.* (2017). European butterfly populations vary in sensitivity to weather across their geographical ranges. *Global Ecology and Biogeography* , 26, 1374–1385.
- Oliver, T.H., Brereton, T. & Roy, D.B. (2013). Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography* , 36, 579–586.
- Oliver, T.H., Roy, D.B., Brereton, T. & Thomas, J.A. (2012). Reduced variability in range-edge butterfly populations over three decades of climate warming. *Global Change Biology* , 18, 1531–1539.
- Oliver, T.H., Stefanescu, C., Paramo, F., Brereton, T. & Roy, D.B. (2014). Latitudinal gradients in butterfly population variability are influenced by landscape heterogeneity. *Ecography* , 37, 863–871.
- Osorio-Olvera, L., Yanez-Arenas, C., Martinez-Meyer, E. & Peterson, A.T. (2020). Relationships between population densities and niche-centroid distances in North American birds. *Ecology Letters* , 23, 555–564.
- Palmer, G., Platts, P.J., Brereton, T., Chapman, J.W., Dytham, C., Fox, R., *et al.* (2017). Climate change, climatic variation and extreme biological responses. *Philosophical Transactions of the Royal Society B: Biological Sciences* , 372, 20160144–20160144.
- Papuga, G., Gauthier, P., Pons, V., Farris, E. & Thompson, J.D. (2018). Ecological niche differentiation in peripheral populations: a comparative analysis of eleven Mediterranean plant species. *Ecography* , 41, 1650–1664.
- Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., *et al.* (2018). Biodiversity increases and decreases ecosystem stability. *Nature* , 563, 109–112.

- Pianka, E.R. (1970). On r- and K-Selection. *The American Naturalist* , 104, 592–597.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2019). *nlme: linear and nonlinear mixed-effects models. R package version 3.1-103* .
- van der Plas, F. (2019). Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews* , 94, brv.12499–brv.12499.
- Poggiato, G., Munkemuller, T., Bystrova, D., Arbel, J., Clark, J.S. & Thuiller, W. (2021). On the Interpretations of Joint Modeling in Community Ecology. *Trends in Ecology & Evolution* , 1–11.
- Pollard, E. & Yates, T. (1993). *Monitoring Butterflies for Ecology and Conservation* . Chapman and Hall, London.
- R Core Development Team. (2019). *R: A language and environment for statistical computing (Version 3.6.1)[Software package]* . Vienna, Austria: R Foundation for Statistical Computing. Retrieved from ...
- Roscher, C., Weigelt, A., Proulx, R., Marquard, E., Schumacher, J., Weisser, W.W., *et al.* (2011). Identifying population- and community-level mechanisms of diversity-stability relationships in experimental grasslands. *Journal of Ecology* , 99, 1460–1469.
- Roy, D.B., Rothery, P., Moss, D., Pollard, E. & Thomas, J. a. (2001). Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology* , 70, 201–217.
- Schmucki, R., Pe'er, G., Roy, D.B., Stefanescu, C., Van Swaay, C.A.M., Oliver, T.H., *et al.* (2016). A regionally informed abundance index for supporting integrative analyses across butterfly monitoring schemes. *Journal of Applied Ecology* , 53, 501–510.
- Settele, J., Kudrna, O., Harpke, A., Kuhn, I., Van Swaay, C., Verovnik, R., *et al.* (2008). *Climatic risk atlas of European butterflies* . Pensoft Sofia.
- Shipley, B. (2000). A New Inferential Test for Path Models Based on Directed Acyclic Graphs. *Structural Equation Modeling: A Multidisciplinary Journal* , 7, 206–218.
- Stefanescu, C., Torre, I., Jubany, J. & Paramo, F. (2011). Recent trends in butterfly populations from north-east Spain and Andorra in the light of habitat and climate change. *J Insect Conserv* , 15, 83–93.
- Taylor, L.R. (1961). Aggregation, Variance and the Mean. *Nature* , 189, 732–735.
- Thibaut, L.M. & Connolly, S.R. (2013). Understanding diversity–stability relationships: towards a unified model of portfolio effects. *Ecology Letters* , 16, 140–150.
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* , 80, 1455–1474.
- Tilman, D. & Downing, J.A. (1994). Biodiversity and stability in grasslands. *Nature* , 367, 363–365.
- Tilman, D., Lehman, C.L. & Bristow, C.E. (1998). Diversity-Stability Relationships: Statistical Inevitability or Ecological Consequence? *The American Naturalist* , 151, 277–282.
- Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994). Habitat destruction and the extinction debt. *Nature* , 371, 65–66.
- Ummenhofer, C.C. & Meehl, G.A. (2017). Extreme weather and climate events with ecological relevance: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences* , 372, 20160135–20160135.
- WallisDeVries, M.F., Baxter, W. & Van Vliet, A.J.H. (2011). Beyond climate envelopes: effects of weather on regional population trends in butterflies. *Oecologia* , 167, 559–571.

Wang, S. & Loreau, M. (2014). Ecosystem stability in space: α , β and γ variability. *Ecology Letters* , 17, 891–901.

White, L., O'Connor, N.E., Yang, Q., Emmerson, M.C. & Donohue, I. (2020). Individual species provide multifaceted contributions to the stability of ecosystems. *Nature Ecology & Evolution* .

White, P. & Kerr, J.T. (2006). Contrasting spatial and temporal global change impacts on butterfly species richness during the 20th century. *Ecography* , 29, 908–918.

Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences* , 96, 1463–1468.

Figure 1

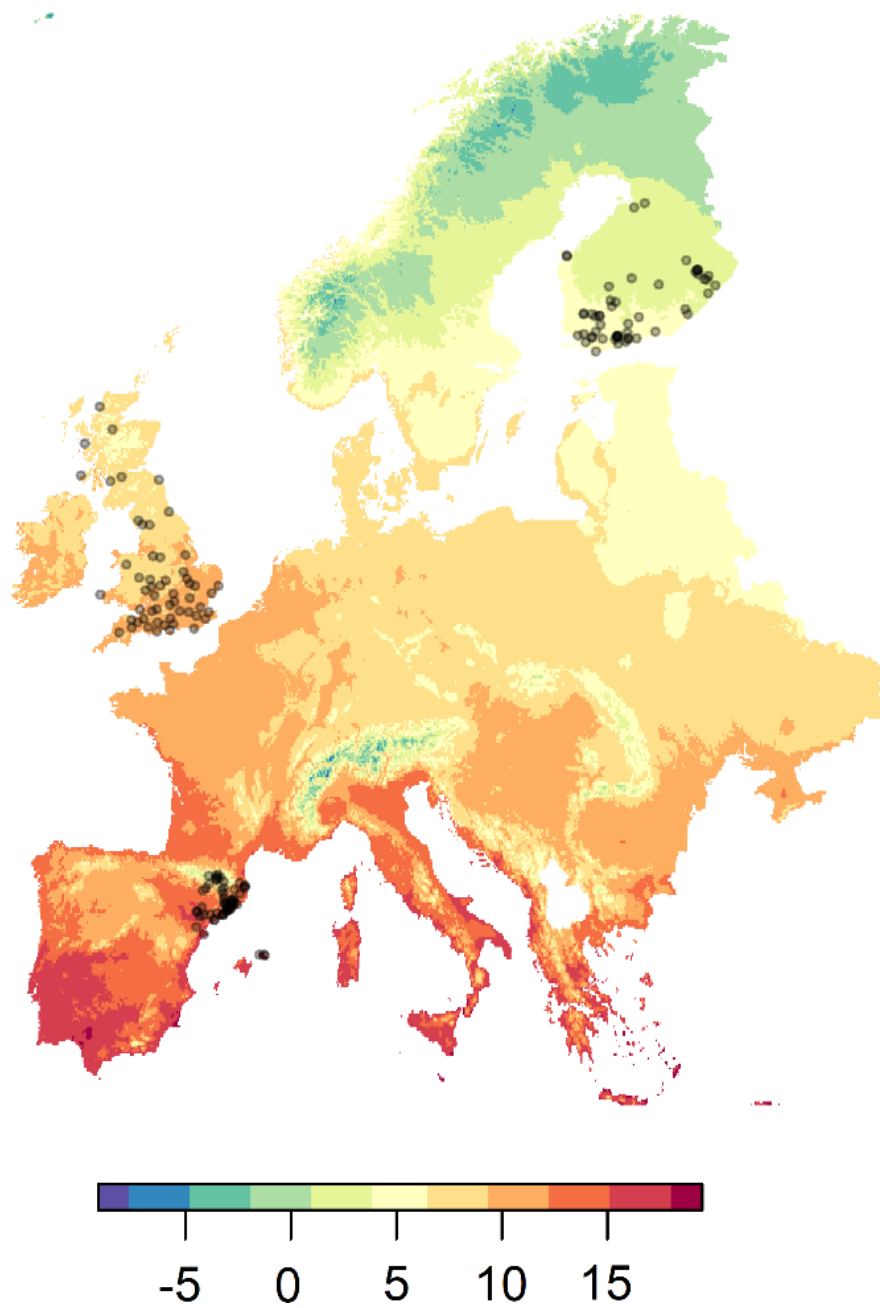


Figure 2

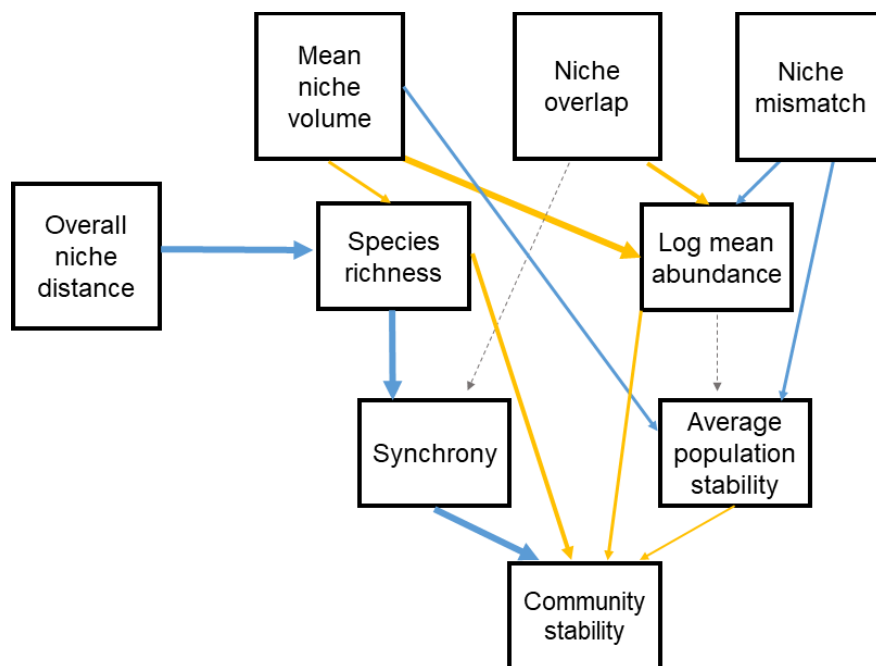


Figure 3

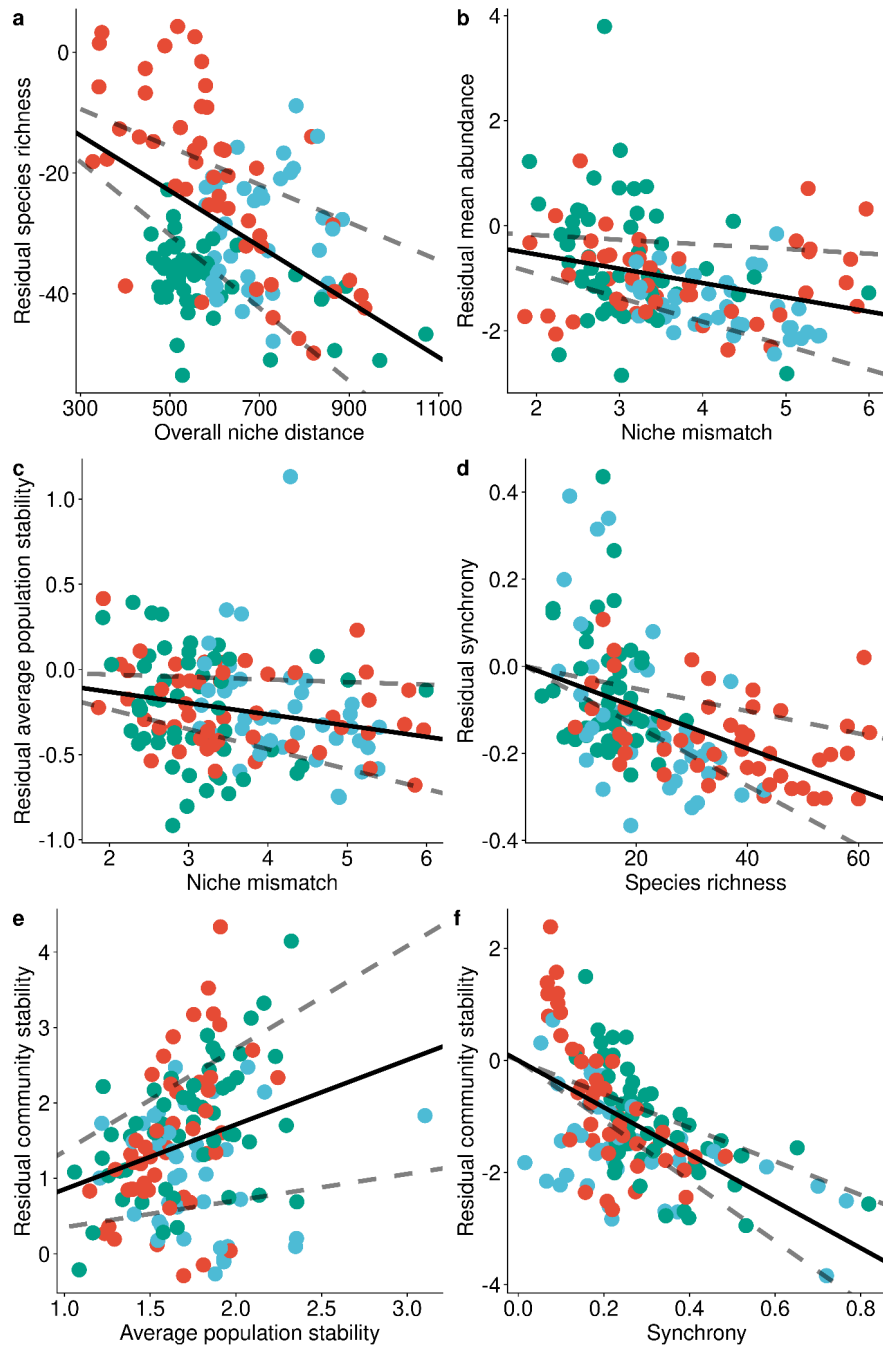


Table 1. Estimated regression parameters from the structural equations model as displayed in Figure 2.

	Estimate	Standardised estimate	Standard error	Critical value	p-value	R-squared
Species richness						0.26
<i>Overall niche distance</i>	-0.046	-0.468	0.0074	-6.171	<0.001	
<i>Mean niche volume</i>	0.016	0.227	0.0068	2.756	0.007	
Log mean abundance						0.18
<i>Niche mismatch</i>	-0.175	-0.229	0.072	-2.438	0.016	

	Estimate	Standardised estimate	Standard error	Critical value	p-value	R-squa
<i>Mean niche volume</i>	0.0016	0.416	<0.001	3.920	<0.001	
<i>Niche overlap</i>	2.562	0.318	0.999	2.564	0.011	
Synchrony						0.23
<i>Niche overlap</i>	0.054	0.035	0.161	0.334	0.739	
<i>Species richness</i>	-0.0047	-0.453	0.001	-4.315	<0.001	
Average population stability						0.10
<i>Niche mismatch</i>	-0.0605	-0.196	0.026	-2.343	0.021	
<i>Mean niche volume</i>	-0.0004	-0.232	<0.001	-2.745	0.007	
<i>Log mean abundance</i>	-0.019	-0.046	0.028	-0.528	0.599	
Community stability						0.52
<i>Average population stability</i>	0.715	0.173	0.248	2.890	0.005	
<i>Synchrony</i>	-4.188	-0.476	0.600	-6.986	<0.001	
<i>Log mean abundance</i>	0.358	0.214	0.100	3.590	0.005	
<i>Species richness</i>	0.028	0.304	0.006	4.482	<0.001	
Correlated errors						
<i>Species richness – niche overlap</i>	-	-0.654	-	-10.217	<0.001	
<i>Species richness – niche mismatch</i>	-	0.226	-	2.745	0.003	

Figure 1. Map of the study extent, colours represent average annual temperatures (°C; bioclimatic variable 1) and black circles show butterfly recording sites, shaded to show any overlap of the points used to represent sites.

Figure 2. Representation of the piecewise structural equation model for testing the five hypotheses along with results. Blue lines represent significant negative associations and yellow lines represent significant positive associations. The thickness of the lines represents the standardised effect size. Dashed lines in grey are non-significant, these were retained as they test elements of the key hypotheses.

Figure 3. Selected relationships tested in the five hypotheses: a) Overall niche distance against species richness, b) Niche mismatch against log mean abundance, c) Niche mismatch against average population stability, d) Species richness against synchrony e) Average population stability against community stability, f) Synchrony against community stability. Lines show models fits and dashed lines 95% confidence intervals. All plots show model fits relative to partial residuals. Point colour represents the countries of the site.