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RESEARCH ARTICLE

Connectivity and climate influence diversity–stability relationships across spatial scales in European butterfly metacommunities

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Abstract

Aim: Anthropogenic-driven biodiversity loss can impact ecosystem stability. However, most studies have only evaluated the diversity–stability relationship at the local scale and we do not fully understand which factors stabilize animal populations and communities across scales. Here, we investigate the role of species dispersal ability, climate, spatial distance and different facets of biodiversity on the stability of butterfly populations and communities across multiple spatial scales.

Location: Primarily Western Europe.

Time Period: 2005–2016.

Major Taxa Studied: Butterflies (Rhopalocera) of Europe.

Methods: We assembled a continent-wide database of European butterflies' abundance and used Structural Equation Modelling to evaluate the direct and indirect effects of multiple stabilizing mechanisms. In parallel, we tested the effect of dispersal

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ability on the stability at multiple spatial scales, using a butterfly mobility index as an indicator of dispersal capacity.

Results: Regional stability strongly reflected local stability, which in turn was driven by both taxonomic and functional α -diversity. Spatial asynchrony was also important for regional stability and it was driven by both functional β -diversity and metapopulation asynchrony, which in turn increased with spatial distance among communities. We observed a positive effect of temperature on functional α -diversity and on local stability, whereas precipitation negatively influenced local diversity. Finally, spatial asynchrony contributed more to the regional stability of less mobile species compared to highly mobile ones, indicating that both extrinsic and intrinsic determinants of connectivity impact regional stability indirectly.

Main Conclusions: Our results demonstrate the importance of local and regional processes for regional stability. However, the relative contribution of spatial asynchrony and metapopulation asynchrony increases with connectivity loss, especially for less mobile species, indicating that landscape management should be tailored depending on the dispersal capacity of organisms. Both local biodiversity loss and regional biotic homogenization destabilize metacommunities, with potential implications for the reliable provision of ecosystem functions.

KEYWORDS

connectivity, dispersal ability, diversity–stability relationships, regional stability, spatial asynchrony, spatial distance

1 | INTRODUCTION

Increasing anthropogenic pressures on Earth are leading to biodiversity loss, which may affect the stability of ecosystem functions and services that humanity depends upon (Schindler et al., 2010). The sense of a biodiversity crisis has prompted hundreds of studies conducted over the last decades, most of them experimental, to investigate the relationship between biodiversity and stability (e.g., Tilman et al., 2006, Loreau & de Mazancourt, 2013, Wilcox et al., 2017). There is now a general consensus that biodiversity is important for ecosystem stability (Loreau et al., 2003; Wang & Loreau, 2016). The stabilizing effect of biodiversity has been mainly linked to two non-exclusive mechanisms: (i) temporal asynchrony of species due to their complementary responses to environmental fluctuations (i.e., the insurance effect, Yachi & Loreau, 1999); and (ii) higher biodiversity increases the likelihood of the presence of species that are tolerant to environmental perturbations (Yachi & Loreau, 1999). However, most studies have focused on local scales, relating α -diversity to the stability of local communities (i.e., local or α -stability, e.g., Tilman et al., 2006, Loreau & de Mazancourt, 2013) and it is unclear what drives the stability of ecosystems from local to regional scales and how different environmental contexts alter diversity–stability relationships at macro-scales (but see Liang et al., 2022 and Qiao et al., 2022).

Analogous to the local species asynchrony that stabilizes local communities, stability at the regional scale (i.e., metacommunity)

can result from spatial asynchrony among local communities' total abundance (Wang & Loreau, 2014). Spatial asynchrony is linked to two main processes. First, higher spatial dissimilarity in species composition (β -diversity) increases the likelihood of complementary responses among communities to a common environmental pressure, which results in asynchronous fluctuations among local communities, thus increasing regional stability (i.e., spatial insurance effect; Wang & Loreau, 2016). Secondly, spatial asynchrony can result from complementary responses among spatially structured subpopulations of the same species (hereafter metapopulation asynchrony) (Wilcox et al., 2017). Such species-level spatial asynchrony (Wang et al., 2019) happens, for instance, when a common and widespread species responds differently to environmental conditions in different habitat patches along environmental gradients. Regional stability can also be observed if every local community is stable, so that local stability directly translates into regional stability, independent of spatial asynchrony (Wang & Loreau, 2016). However, there is no consensus yet on whether local stability or spatial asynchrony is the main driver of regional stability (Wang & Loreau, 2014). Both mechanisms are likely relevant (Appendix S1, Figure S1.1) but may vary in significance depending on the environmental context and spatial scale (Qiao et al., 2022; Wilcox et al., 2017). It is an important next step to determine under which circumstances and environmental contexts local or regional mechanisms become more important in stabilizing metacommunities.

There is evidence that increasing the spatial extent of metacommunities leads to a higher relative contribution of spatial asynchrony to regional stability compared to local stability (Liang et al., 2022). This is expected because β -diversity generally increases with the spatial distance among local communities (Soininen et al., 2007) and because higher β -diversity enhances spatial asynchrony among local communities (Catano et al., 2020; Wang et al., 2021). However, it is important to consider that dispersal limitation does not only depend on landscape structural connectivity but also on ecological differences among species and individuals (e.g., Auffret et al., 2017). Therefore, it is crucial to test empirically how species traits linked to dispersal capacity influence regional stability through their effect on β -diversity and spatial asynchrony. From an applied perspective, a higher importance of β -diversity and spatial asynchrony for regional stability compared to local processes (e.g., Catano et al., 2020; Qiao et al., 2022), would imply a stronger focus on the preservation of multiple sites within the landscape to reduce variability in ecosystem processes and services. Conversely, if α -diversity and local stability are more important (Wang et al., 2021; Wilcox et al., 2017), priority should be given to preserving sites that are more diverse and stable locally.

Although spatial asynchrony can also result from β -diversity and from metapopulation asynchrony, the latter mechanism has received less attention in studies on diversity–stability relationships across scales (but see Wilcox et al., 2017). Metapopulation asynchrony can be influenced by the differential responses of local populations to environmental factors (Thorson et al., 2018). These variations in local population responses may be attributed to phenotypic plasticity (Brans et al., 2017) and other spatial, connectivity-related mechanisms, including genetic differences resulting from geographic isolation (Orsini et al., 2013) and priority effects (de Meester et al., 2016). For instance, an experimental study that manipulated dispersal rates among populations of *Drosophila* found that limited dispersal enhanced metapopulation stability due to asynchronous responses among sub-populations (Dey & Joshi, 2006). Thus, it is also important to consider how spatial distances and species traits linked to dispersal ability influence metapopulation dynamics and their effects on spatial asynchrony.

Animal ecology studies on diversity–stability relationships across scales are still rare (but see Catano et al., 2020), especially due to a lack of high-resolution abundance data covering large spatial extents. Thanks largely to the work of community science, European butterflies can be considered an excellent model group, because they have been systematically monitored in several countries spanning a considerable latitudinal and climatic gradient (van Swaay et al., 2008). In addition, butterflies are particularly sensitive to climate change and land use (Parmesan, 2003; Thomas, 2005), which are factors that might affect their abundance and stability. Compared to other insect groups, we have considerable knowledge about the functional traits, phylogeny, biology and ecology of butterflies, especially in Europe (Settele et al., 2009). Consequently, investigating the mechanisms influencing the stability of butterfly populations across different spatial scales is now feasible and can

provide insights into the conservation of other insects, which often lack detailed abundance and trait data (Stork, 2018).

Here, we assembled a large database of butterfly abundances with high spatial resolution gathered across seven European countries to test the influence of geographic and climatic variables, species dispersal capacity as well as functional and taxonomic-based diversity metrics on regional stability. Particularly, we aimed at testing the following hypotheses: (H1) α -diversity stabilizes overall butterfly abundances within local communities, which scales up to influence regional stability. Particularly, we expect that communities with higher taxonomic and functional α -diversity will be characterized by higher local species asynchrony in response to environmental fluctuations than communities with lower α -diversity (Yachi & Loreau, 1999, Figure 1, Appendix S1 and Table S1.1). Since α -diversity is generally positively related to dispersal (e.g., Cadotte, 2006), we expect higher α -diversity for highly mobile species compared to less mobile species. (H2) Taxonomic and functional β -diversity increases spatial asynchrony among local communities and, consequently, this spatial asynchrony translates into regional stability (Polley et al., 2020, Liang et al., 2022, Figure 1, Appendix S1 and Table S1.1). We expect that less mobile species will have higher spatial β -diversity owing to dispersal limitation than more mobile species. (H3) As metapopulation asynchrony can also increase spatial asynchrony and thus regional stability, we expect populations of the same species in different local communities to exhibit asynchronous dynamics (Wilcox et al., 2017, Figure 1, Appendix S1 and Table S1.1). However, we expect that spatially structured populations of more mobile species will have less metapopulation asynchrony than less mobile species. (H4) Spatial distance increases taxonomic and

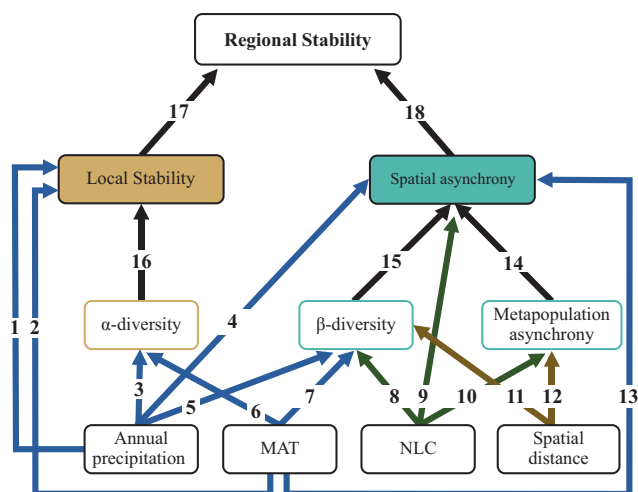


FIGURE 1 Conceptual model showing the pathway network used to test the direct and indirect effects of abiotic factors, biodiversity and mechanisms that promote stability at multiple spatial scales. The blue, green, brown and black arrows indicate positive effects of climate, number of local communities (NLC), spatial distance and biodiversity respectively. MAT stands for mean annual temperature. Each pathway is numbered and described in Appendix S1 and Table S1.1.

functional β -diversity and thus the probability of asynchronous fluctuations between local communities (Figure 1, Appendix S1 and Table S1.1). We expect that spatial distance will increase both β -diversity and spatial asynchrony, due to higher dispersal limitation and environmental heterogeneity among communities (Larsen et al., 2021). This should particularly apply to less mobile species, where spatial distance is more likely to translate into dispersal limitation than for highly mobile species. (H5) Spatial variation in climatic factors, such as precipitation and temperature, positively modulate the stabilizing effect of biodiversity at multiple scales because these variables can promote β -diversity of plants (Zellweger et al., 2017) and stability of plant biomass (Liang et al., 2022; Wang et al., 2021), including butterfly host plants, contributing to the β -diversity of butterfly communities (Zellweger et al., 2017, Figure 1, Appendix S1 and Table S1.1).

2 | METHODS

2.1 | Data selection

We extracted butterfly data from the long-term community science European Butterfly Monitoring Scheme (eBMS, van Swaay et al., 2022). All monitoring schemes are based on standardized Pollard-walk transects (Pollard, 1977; van Swaay et al., 2015) surveyed weekly during the main butterfly activity period (March to October) under beneficial weather conditions (see van Swaay et al., 2015 for more details). Since transects varied in length and were composed of several nested sections of variable length, we aggregated contiguous sections along each transect to generate comparable sampling lengths of approximately 200m (mean \pm SD = 203.7 \pm 11.6), covering Spain, France, Germany, Luxembourg, Belgium, The Netherlands, The United Kingdom, Sweden, and Finland. The dataset comprised the period from 2005 to 2016, which was the time window that maximizes data availability for all countries mentioned above. Subsequently, only transect sections that were revisited three or more months per year were used ($n=1105$) and the average abundance per species and year was calculated and used as an estimate of annual species abundance. Each aggregated section (approximately 200m) of transect was considered a local community. For the selection of metacommunities, we first plotted a grid with 20 \times 20 km cells on the map of Europe (Appendix S1 and Figure S1.2). We then selected metacommunities that had three to five communities within a grid cell, monitored for a minimum of four and a maximum of twelve consecutive years. In the case that there were more than five local communities within a grid cell, we randomly selected only four or five sections to have a more balanced sampling effort (i.e., ranging from three to five local communities in all metacommunities). After this procedure, 285 metacommunities were retained for analysis. None of them were in the territories of Sweden and Luxembourg. This is because their communities and/or metacommunities did not meet all the pre-established criteria prior to the analyses. Since the countries started the monitoring scheme in different years, we only

analysed communities with the same monitoring time within each metacommunity (minimum of four and maximum of twelve consecutive years). After a simple linear regression performed with the 'lm' function of the R v.4.2.2 (R Core Team, 2022), we confirmed that the number of consecutive years did not influence the stability measure of the metacommunities ($R^2_{\text{adjusted}} = -0.0033$, $F = 0.07$, $p = 0.79$), justifying this procedure.

2.2 | Calculation of stability components

For each metacommunity, we calculated the regional stability of butterfly species abundance, following the model developed by Wang and Loreau (2014, 2016). For this, we use the average species abundance per year. Moreover, we calculated the inverse of variability and synchrony metrics to represent stability and asynchrony respectively (see Wilcox et al., 2017). The formulas used to calculate each metric are presented below:

$$\text{Regional stability} = \frac{\mu_M}{\sigma_M} \quad (1)$$

where μ_M is the temporal mean of annually summed total abundance in metacommunity M and σ_M is the temporal standard deviation.

Spatial asynchrony is the degree to which the total abundance of butterflies from different local communities fluctuates differently from one another through time (see Hautier et al., 2020):

$$\text{Spatial asynchrony} = \frac{\sum_i \sqrt{w_{ii}}}{\left(\sqrt{\sum_{ij} w_{ij}} \right)} \quad (2)$$

where w_{ii} denotes the variance of total abundance in community i , and w_{ij} denotes the covariance in total abundance between community i and j .

Local stability is the temporal average of the stability of butterfly abundance at the local community scale. This metric, for each local community, was obtained by calculating the coefficient of temporal variation of the total abundance of the community in each transect, weighted by the abundance of the local community and taking the inverse, according to Wilcox et al. (2017):

$$\text{Local community stability} = \left(\sum_i \frac{\mu_i}{\mu_M} \times \frac{\sigma_i}{\mu_i} \right)^{-1} \quad (3)$$

where μ_i is the temporal mean of the total abundance in the community i , μ_M is the temporal mean of the total abundance in the metacommunity M and σ_i is the temporal standard deviation of the total abundance in the community i .

$$\text{Metapopulation asynchrony} = \left(\frac{\sum_{m,n} w_{mn}}{\left(\sum_m \sqrt{w_{mm}} \right)^2} \right)^{-1} \quad (4)$$

where for each species i present within a metacommunity, w_{mn} is the temporal covariance between populations m and n and w_{mm} is

the temporal variance of population m , as referenced from a covariance matrix. This metric is then averaged across species, weighted by species' relative abundances, to obtain a single value for each metacommunity.

2.3 | Calculating taxonomic and functional α -diversity and β -diversity

We calculated the average taxonomic α -diversity per metacommunity, using the inverse of Simpson's index, obtained by the 'diversity' function of the 'vegan' R-package (Oksanen et al., 2022). To calculate functional α -diversity and β -diversity indices, we used two important life-history traits of butterflies: (i) wingspan, which is related to longevity and fecundity and is considered as an important response trait to certain environmental factors such as temperature (Chown & Gaston, 2010; Merckx et al., 2018); and (ii) egg volume, related to survival, performance of immature stages and number of food plant genera (García-Barros, 2000). Trait data were obtained from Essens et al. (2017) and analysed for the existence of collinearity, using the following criteria: Pearson correlation test ($r < 0.7$) and variance inflation factor (VIF) < 3 (Zuur et al., 2010). For the calculation of functional α -diversity, we initially subjected the species \times trait matrix to a clustering procedure using UPGMA with Gower distances to produce a dendrogram. Next, we used a species \times sites matrix with abundance data and the dendrogram produced by the clustering process, as arguments of the 'alpha' function of the 'BAT' R-package (Cardoso et al., 2022). Finally, we calculated the mean functional α -diversity of the communities to obtain a single value for each metacommunity. Regarding the calculation of spatial taxonomic β -diversity, we used the ratio between γ -diversity (also based on the inverse of Simpson's index) and the mean of taxonomic α -diversity. The pairwise functional β -diversity was calculated using the 'beta' function from the 'BAT' R-package (Cardoso et al., 2022), using species abundances and trait matrices for functional α -diversity. All diversity metrics, at different scales, were calculated for each year of the time series and then averaged across years to represent long-term estimates. Moreover, we decided to use the inverse of Simpson's index to calculate α , γ and β -taxonomic diversity to make this study comparable with other studies on biodiversity-stability relationships at multiple scales, which used the same methodology but with taxonomic data only.

2.4 | Calculating spatial distance

To obtain a single value of spatial distance between all local communities per metacommunity, we used the mean of the pairwise Euclidean distance weighted by the mean pairwise shortest topographic distance (Wang, 2020), to account for potential dispersal barriers. These metrics were calculated using the geographic coordinates of the centroid of each local community (decimal degrees,

unit in meters) and the elevation layer from WorldClim at 10-min resolution.

2.5 | Climatic data

Mean annual precipitation (MAP) and mean annual temperature (MAT) layers were obtained from the WorldClim bioclimatic variables version 2 (1970–2000) at 10-min resolution (<http://www.worldclim.org/>, Hijmans et al., 2005). We averaged the MAP and MAT per metacommunity grid cell to obtain a single value. Thus, these metrics represent the spatial variation in temperature and precipitation between metacommunities.

2.6 | Classifying butterfly species into low and high mobility categories

Based on the mobility index proposed by Essens et al. (2017), which takes into account available information on dispersal ability for a large number of species and combines it with information on range size, wingspan and voltinism to estimate dispersal capacity for the remaining taxa, we classified butterfly species into two groups: (i) low and (ii) high mobility. Low mobility species ($n = 81$) are those that fell below the median value of the mobility index, whereas high mobility species ($n = 112$) are those equal to or above the median. However, to ensure a more balanced number of species between the butterfly groups for further analysis (see below), we excluded the 31 least mobile species from the highly mobile group (i.e., those closer to the median). Here, we also selected the traits (wingspan and egg volume) to calculate functional α -diversity and β -diversity indices of each mentioned group. The correlation between these two traits was weak according to Pearson's correlation test ($r < 0.7$) and VIF < 3 (Zuur et al., 2010), both for the low mobility species ($r = 0.51$ and VIF = 1.60) and the high mobility species ($r = 0.62$ and VIF = 1.43). We also carried out the same analyses between wingspan and mobility. We obtained the following results: (i) $r = 0.16$ and VIF = 1.02 for low mobility species and (ii) $r = 0.11$ and VIF = 1.02 for high mobility species. It is noteworthy that the comparative analyses between the two groups were carried out considering the same period and the same study sites. As a result, the number of less mobile species fell from 81 to 78.

2.7 | Statistical analyses

Based on theoretical and empirical studies on the stability-diversity relationship (e.g., Catano et al., 2020; Liang et al., 2022; Wang & Loreau, 2016), we developed an initial theoretical model (Figure 1), considering ecologically reasonable links (Appendix S1 and Table S1.1). To test the significance and strength of the hypothesized direct and indirect stabilizing effects of each

component included in the initial model, we used structural equation modelling (SEM). Moreover, since different grid cells (meta-communities) can vary in the number of local communities (NLC) from 3 to 5, we considered it important to include this variable in the initial model. This variable can also influence β -diversity as well as metapopulation and spatial asynchrony, as demonstrated in recent studies (Catano et al., 2020; Liang et al., 2022; Wang & Loreau, 2014). We natural-log (\log_e) transformed all variables to improve normality and fitted linear-based SEM models using the 'piecewiseSEM' R-package (Lefcheck, 2016). Importantly, the logarithmic transformation caused the variance of regional stability to be fully explained by local stability and spatial asynchrony (Wang et al., 2021). We started by building an initial SEM with data from the entire set of species (i.e., combining both low and high mobile species) and using the taxonomic indices of α - and β -diversity. Then, we built another SEM but replaced the taxonomic indices of α - and β -diversity to their functional counterparts. We performed the same procedures focusing on the low and high mobility species separately. Thus, in total, we performed six initial SEMs, analysing: (i) the entire dataset based on taxonomic and functional diversity indices; (ii) low mobility species based on taxonomic and functional diversity indices, and (iii) high mobility species based on taxonomic and functional diversity indices. However, none of our six hypothesized SEM models were supported by the data (i.e., poor model fit, with Fisher's C and Chi-squared $p < 0.05$, see Appendix S1, legends to Figures S1.3 and S1.4). We then followed the approach set out by Catano et al. (2020), Liang et al. (2022), Zuo et al. (2023) and others, which consists of carrying out an exploratory path analysis to find a model with a satisfactory fit. Firstly, based on Shipley's d-separation test, we considered potential correlated errors, which are unforeseen correlations between variables that do not have a clear causal link (Lefcheck, 2016; e.g., correlation between metapopulation asynchrony and local stability). Secondly, we removed statistically non-significant links ($p > 0.05$) if this would improve the fit of the model ($\chi^2 > 0.05$ and Fisher's C > 0.05 , see Catano et al., 2020, Liang et al., 2022). In addition, we checked for residual spatial autocorrelation in our final SEM models by calculating Moran's I and there was none (see Tallavaara et al., 2018). Although the final six models showed better fits, it is important to note that this was determined based on the structure of the data. Finally, to assess the relative importance of local stability and spatial asynchrony to regional stability, we partitioned their variances ('varpart' function, 'vegan' R-package) by means of partial regressions, allowing the quantification of the unique and shared contribution of both predictors.

To compare the stability and diversity patterns among meta-communities composed of highly mobile and relatively less mobile species, we ran several permutational univariate analyses of variance (permutational ANOVA, 5000 iterations). To do so, we used mobility as a factor (low and high) and considered the following descriptors as dependent variables, one at a time: (i) taxonomic α -diversity; (ii) functional α -diversity; (iii) taxonomic β -diversity; (iv) functional β -diversity; (v) metapopulation asynchrony; (vi) spatial

asynchrony; (vii) local stability and (viii) regional stability. For this test, we used the function 'aovp' from the 'lmPerm' R-package (Wheeler & Torchiano, 2016). All analyses were performed in the R software environment version 4.2.2 (R Core Team, 2022). Code and data that support the results are available at doi.org/10.6084/m9.figshare.24716334.

3 | RESULTS

3.1 | Importance of local stability and spatial asynchrony for regional stability

According to SEMs built on the basis of the entire dataset (Figure 2a,b), the metacommunity level stability of European butterflies was more influenced by the stability of local communities [standardized path coefficient (spc)=0.71, $p < 0.001$] than by spatial asynchrony (spc=0.58, $p < 0.001$; see also Appendix S1 and Figure S1.5).

3.2 | Positive effects of butterfly species diversity on stability at multiple scales

Considering the entire dataset, we observed a positive influence of taxonomic and functional α -diversity on local community stability (Figure 2a,b). Additionally, the magnitude of such positive effects of both α -diversity facets was quantitatively similar (spc=0.32, $p < 0.001$, taxonomic and spc=0.28, $p < 0.001$, functional). Taxonomic β -diversity was not significantly related to spatial asynchrony among local communities (spc=-0.04, $p = 0.46$). By contrast, functional β -diversity (spc=0.13, $p < 0.01$) and, especially, metapopulation asynchrony (spc=0.63, $p < 0.001$, Figure 2a) positively influenced spatial asynchrony among local communities. The effects of taxonomic and functional α -diversity on local community stability as well as the effects of metapopulation asynchrony and functional β -diversity on spatial asynchrony propagated across scales to indirectly influence the stability of metacommunities (Figure 2a,b).

3.3 | Importance of spatial distance, climatic factors and number of local communities on stability at multiple scales

Considering the entire dataset, we found that spatial distance increased spatial asynchrony among communities indirectly through metapopulation asynchrony (spc=0.41, $p < 0.001$, Figure 2a,b) and functional β -diversity (spc=0.42, $p < 0.001$, Figure 2b), but not through taxonomic β -diversity (Figure 2a). Climatic factors influenced regional stability only through local stability (Figure 2a) and taxonomic and functional α -diversity, but not through any measurement of β -diversity (Figure 2a,b). Specifically, temperature had

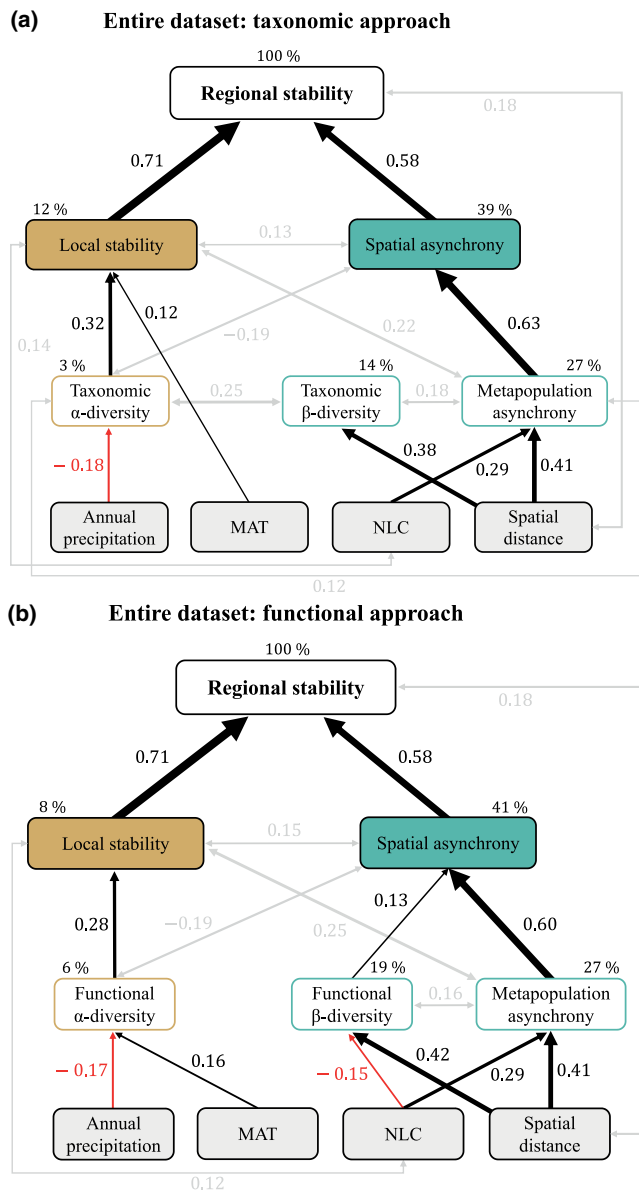


FIGURE 2 Results of structural equation modelling (SEM) showing direct and indirect pathways through which local and spatial factors determine regional stability of European butterfly abundance. The final SEM (a) based on multiplicative taxonomic β -diversity and local mean species diversity (inverse Simpson's index) and (b) based on pairwise functional β -diversity and local mean functional diversity. Black arrows indicate positive effects ($p < 0.05$), red arrows represent negative effects ($p < 0.05$) and grey double-headed arrows represent covariant variables. The numbers adjacent to the arrows are standardized path coefficients, and the width of the arrows indicates the strength of the relationship. The percentages next to the variables indicate the variance explained by the model (R^2). The SEM statistics were as follows: (a): $\chi^2 = 31.0$, $df = 23$, $p = 0.12$; Fisher's $C = 45.0$; $df = 44$, $p = 0.43$; (b): $\chi^2 = 32.7$, $df = 24$, $p = 0.11$ and Fisher's $C = 42.4$, $df = 44$; $p = 0.54$ (indicating good model data fit).

a positive influence on local stability ($spc = 0.12$, $p < 0.05$, Figure 2a) and functional α -diversity ($spc = 0.16$, $p < 0.01$, Figure 2b). On the other hand, the effect of precipitation on both the taxonomic

($spc = -0.18$, $p < 0.01$, Figure 2a) and functional ($spc = -0.17$, $p < 0.01$, Figure 2b) facets of α -diversity was negative. Finally, we observed that the NLC had a negative impact on functional β -diversity ($spc = -0.15$, $p < 0.01$, Figure 2b) and a positive influence on metapopulation asynchrony ($spc = 0.29$, $p < 0.001$, Figure 2a,b). With regard to the taxonomic facet of β -diversity, the NLC showed no effect ($spc = 0.002$, $p = 0.98$).

3.4 | Impact of species dispersal ability on stability at multiple scales

On average, metacommunities of relatively less mobile species were characterized by significantly lower taxonomic α -diversity and functional α -diversity compared to the metacommunities of relatively more mobile species ($p < 0.001$, Figure 3a,b). Taxonomic β -diversity was on average significantly higher for metacommunities of more mobile species ($p < 0.01$, Figure 3c). By contrast, functional β -diversity was significantly higher for relatively less mobile species ($p < 0.001$, Figure 3d). Metapopulation asynchrony and spatial asynchrony were both higher for metacommunities of less mobile species ($p < 0.001$, Figure 3e,f). Local stability and regional stability of butterfly abundances were significantly higher in the group of species with relatively higher dispersal capacity ($p < 0.001$, Figure 3g,h).

Compared to the group of less mobile species, we observed a small increase in the relative contribution of local stability to regional stability in the group of highly mobile species (change in spc from 0.71 in the low mobility group to 0.76 in the group of high mobility, Figure 4). In contrast, we observed a small increase in the relative contribution of spatial asynchrony to regional stability in the group of less mobile species compared to the group of highly mobile ones (change in spc from 0.47 in the high mobility group to 0.55 in the group of less mobile species; Figure 4). We also found that metapopulation asynchrony ($spc = 0.80$, $p < 0.001$, Figure 4a,c) contributed more to both spatial asynchrony and regional stability of low mobility butterflies when compared to the highly mobile species group ($spc = 0.64$, $p < 0.001$, Figure 4b,d). Moreover, we observed that the relative contribution of taxonomic α -diversity to local stability was similar for both species' groups [$spc = 0.38$, $p < 0.001$ (low mobility species, Figure 4a) and $spc = 0.40$, $p < 0.001$ (high mobility species, Figure 4b)]. On the other hand, the functional α -diversity of the less mobile butterflies showed a slightly stronger positive relationship with local stability ($spc = 0.38$, $p < 0.001$, Figure 4c) compared to the more mobile group ($spc = 0.34$, $p < 0.001$, Figure 4d). Finally, we found that no facet of β -diversity was relevant to the spatial asynchrony of low- and high-mobility species.

We also carried out the same analyses using 112 more mobile species, that is, without removing any species from the highly mobile group. The results were very similar to those obtained using metrics of 81 species (Appendix S1 and Figure S1.7a,b). Furthermore, the strength of the relationships was very similar in both datasets. The unstandardized effects, standard errors and p -values of each

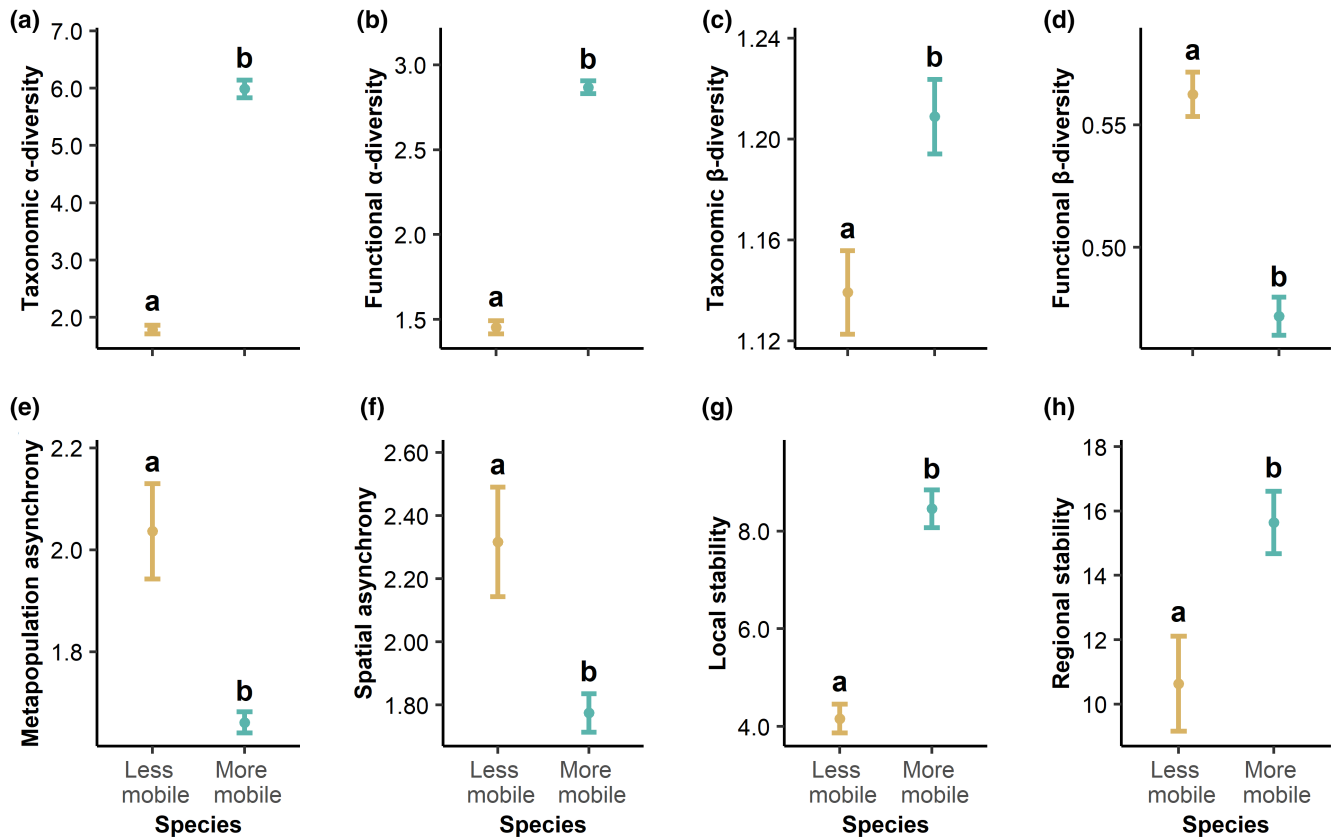


FIGURE 3 Error bars with means and standard errors for diversity and stability metrics of low (brown error bars) and highly mobile (blue error bars) European butterfly species. (a) taxonomic α -diversity, (b) functional α -diversity, (c) taxonomic β -diversity, (d) functional β -diversity, (e) metapopulation asynchrony, (f) spatial asynchrony, (g) local stability and (h) regional stability. Distinct letters (a versus b) indicate significant differences ($p < 0.05$) based on permutational ANOVA.

significant link have been provided in Appendix S1 and Tables S1.2, S1.3, S1.4 and S1.5.

4 | DISCUSSION

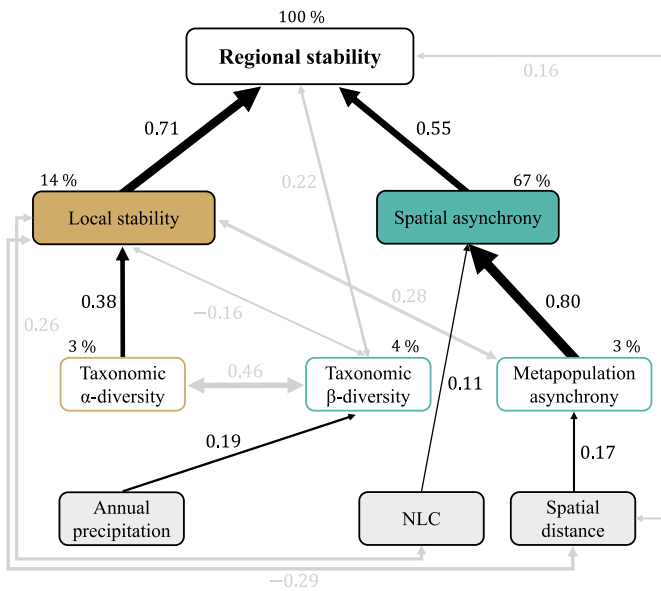
Here, we used a high-resolution dataset of butterflies gathered in seven European countries and covering several years to investigate diversity–stability relationships across spatial scales. We demonstrate that both α -diversity and β -diversity played significant roles in stabilizing metacommunities, through their direct effects on local stability and spatial asynchrony respectively. Moreover, we also observed a direct positive effect of temperature on functional α -diversity and local stability. In contrast, we observed a direct and indirect negative effect of precipitation on local diversity and on the stability of local communities respectively. Additionally, we also show for the first time that differences in dispersal capacity among species can influence the relative importance of local stability and spatial asynchrony for regional stability of butterflies, as we expected. We note that local stability was the main driver of regional stability for both high and low mobility species. This implies that local processes prevail, but spatial dynamics should not be entirely disregarded when designing landscape management

strategies, especially when the focus is the stability of less mobile species compared to highly mobile ones. When focusing on the entire dataset, we found that using a functional trait-based index of β -diversity improves predictions of spatial asynchrony and regional stability when compared to taxonomic β -diversity. Metapopulation asynchrony contributed more to spatial asynchrony in abundances among communities than metrics of β -diversity. However, there was no clear difference in predictive power between taxonomic and functional-based indices of α -diversity, except when considering the most mobile species. Below, we discuss these findings in more detail.

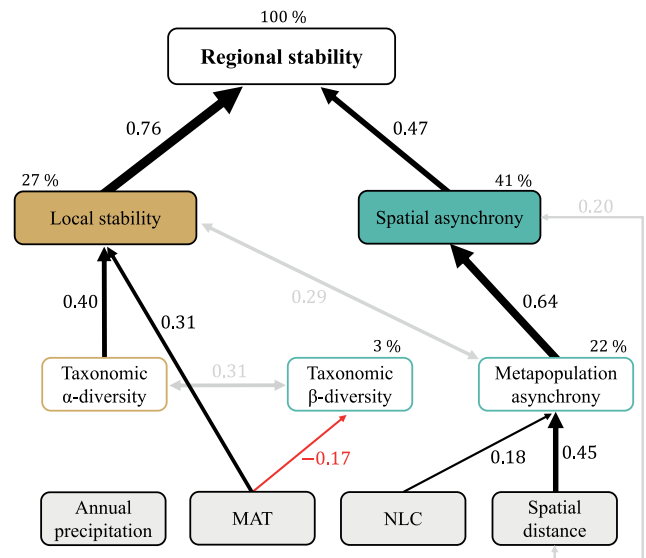
4.1 | Drivers of diversity–stability relationships across scales: The entire dataset

When analysing the drivers of regional stability of European butterfly abundance, we observed that both local stability and spatial asynchrony were important stabilizing mechanisms, but with relatively greater importance of local stability. This result aligns with recent research on plant biodiversity and biomass stability (Hautier et al., 2020; Wilcox et al., 2017), but contrasts with studies on fishes (Thorson et al., 2018) and birds (Catano et al., 2020) where spatial asynchrony was identified as the primary stabilizing factor. A

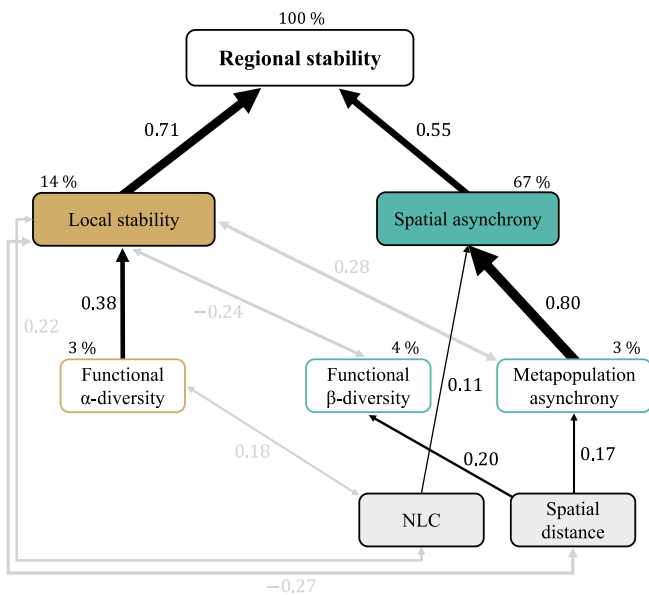
(a) Less mobile species: taxonomic approach



(b) More mobile species: taxonomic approach



(c) Less mobile species: functional approach



(d) More mobile species: functional approach

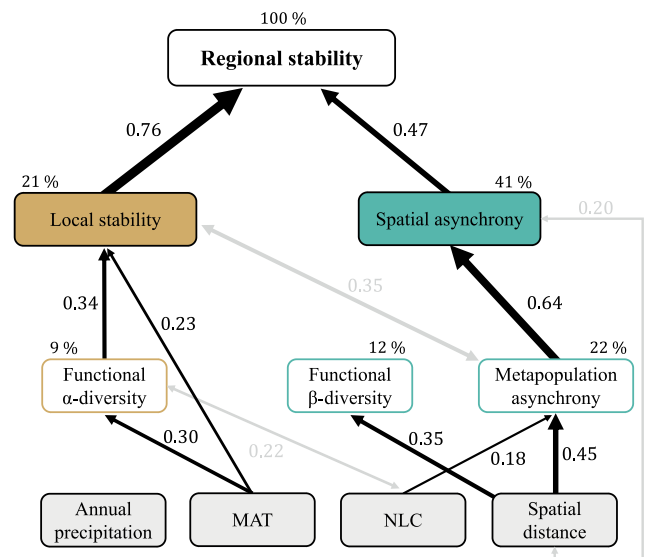


FIGURE 4 The final SEMs (a) and (b) based on multiplicative taxonomic β -diversity and local mean species diversity (inverse Simpson's index) of relatively less mobile and more mobile species respectively; (c) and (d) based on pairwise functional β -diversity and local mean functional diversity of low and high mobility species respectively. Black arrows indicate relationships between measured variables or positive effects ($p < 0.05$), red arrows represent negative effects ($p < 0.05$) and grey double-headed arrows represent covariant variables. The numbers adjacent to the arrows are standardized path coefficients, and the width of the arrows indicates the strength of the relationship. The percentages next to the variables indicate the variance explained by the model (R^2). The SEM statistics were as follows: (a) $\chi^2 = 22.4$, $df = 17$, $p = 0.17$; Fisher's $C = 37.6$; $df = 32$; $p = 0.23$; (b) $\chi^2 = 36.7$, $df = 20$, $p = 0.01$; Fisher's $C = 40.5$; $df = 38$; $p = 0.36$; (c) $\chi^2 = 23.7$, $df = 14$, $p = 0.05$; Fisher's $C = 39.8$; $df = 28$; $p = 0.07$ and (d) $\chi^2 = 39.0$, $df = 24$, $p = 0.03$; Fisher's $C = 44.0$; $df = 42$; $p = 0.39$.

plausible explanation for contrasting influences of local stability and spatial asynchrony are differences in spatial extent among studies. For example, the results of Liang et al. (2022) indicate that the stabilizing effect of spatial asynchrony on regional stability increased with increasing spatial extent, suggesting that spatial asynchrony of biomass may be driven by factors related to spatial distance, such as the environmental heterogeneity, dispersal limitation and

the compositional dissimilarity between local communities (Wang & Loreau, 2014), which tend to increase with geographic distance (Soininen et al., 2007). This lack of consensus among these studies demonstrates the need for more long-term studies that investigate how varying environmental contexts, spatial scales and intrinsic organisms' traits, such as dispersal ability, could affect the relative importance of local and regional stabilizing mechanisms.

We found that both taxonomic and functional α -diversity increased the local stability of butterflies' abundance, which then scaled up to influence regional stability. This result agrees with theoretical models (Loreau & de Mazancourt, 2013; Wang & Loreau, 2016) and empirical studies that reported similar relationships (Bai et al., 2004; Catano et al., 2020; Wang et al., 2021). When we considered the mechanisms underlying local stability (see Appendix S1 and Figure S1.6a,b), we found that both local species stability and species asynchrony influenced local stability with relatively high magnitude. However, it is important to note that while α -diversity had a strong stabilizing role through species asynchrony (see Appendix S1 and Figure S1.6a,b), it explained a relatively small fraction of local stability (small R^2), which means that other unmeasured variables could also be important. In a recent study with European butterflies, Evans et al. (2023) found that species synchrony decreased butterfly community stability, that is, a similar result to ours when considering only local scale processes. Our results go beyond those of Evans et al. (2023), as we also assessed metacommunity stability and linked this to spatial asynchrony among communities in many European landscapes, along with spatial distance, functional diversity and species mobility. Interestingly, we also observed that both taxonomic and functional α -diversity positively influenced only local species asynchrony, but not local species stability (Appendix S1 and Figure S1.6a,b). These findings suggest that butterfly taxonomic and functional α -diversity are good predictors of species response traits, which influence how species respond to environmental perturbations (Loreau & de Mazancourt, 2013).

Traits such as wingspan and egg volume can confer adaptive advantages to butterflies, influencing the fecundity, survival and longevity of individuals (Fischer et al., 2003, 2006; García-Barros, 2000). These factors, in turn, can be essential for the components of the regional stability of butterflies. For example, species with larger eggs that contain greater amounts of energy and water (Fischer et al., 2006; Karl et al., 2007) contribute to the fitness of the immature stages of butterflies under stressful environmental conditions (García-Barros, 2000). However, a comprehensive analysis indicated that there is a trade-off between the number of eggs and egg volume across species (García-Barros, 2000), which is a common pattern related to R and K life-history strategies. While R strategists can rapidly re-colonize sites after disturbances and thus show high resilience to environmental fluctuations, K strategists might be superior competitors. In addition, larger butterflies tend to use large or structurally complex food plants compared to smaller species (García-Barros, 2000). Such complementary food preferences and life-history strategies can thus explain why higher functional diversity locally enhances local stability due to local species asynchrony in the entire dataset. Likewise, spatial complementarity due to shifts in size and egg volume among communities (i.e., functional β -diversity) seems to enhance spatial asynchrony in the entire dataset. The reason why functional α -diversity and β -diversity become non-significant when we analyse low and high mobility species separately is probably due to a more limited range in the two traits within

each of these groups compared to the entire dataset. An important avenue for future research is to evaluate whether butterfly response traits, such as the ones considered here, are also associated with impact traits and ecosystem processes such as pollination and herbivory.

We found that functional β -diversity, but not taxonomic β -diversity, positively influenced spatial asynchrony and, thus indirectly contributed to regional stability. The absence of a stabilizing effect of taxonomic β -diversity in our study coincides with the results of other recent studies that focused on plants (Wilcox et al., 2017; Zhang et al., 2019). The lack of predictive power for taxonomic β -diversity in other studies as well as in ours suggests that functional trait-based indices of β -diversity might be more appropriate to capture spatial variation in ecological aspects that determine differential community responses to a common environmental pressure at a landscape scale, which leads to spatial asynchrony. In this way, our results corroborate the hypothesis of spatial biodiversity insurance (Loreau et al., 2003; Wang & Loreau, 2016), mediated by spatial variation in species traits. It is important to mention that some studies have recently reported an influence of taxonomic β -diversity on spatial asynchrony (Catano et al., 2020; Hautier et al., 2020; Liang et al., 2022; Qiao et al., 2022; Wang et al., 2021), which suggests that the predictive power of taxonomic and/or functional β -diversity might vary depending on which traits were measured and also on the level of functional redundancy. If variation in species composition among communities is not accompanied by variation in functional traits due to high functional redundancy (see Villéger et al., 2013), then it is possible that taxonomic β -diversity will be uninformative. In such a case, it would be better to use metrics of functional β -diversity informed by relevant traits as a way to distinguish between scenarios of high functional redundancy and high functional complementarity among communities (Mouchet et al., 2010). As far as we are aware, this is the first study to demonstrate a positive association between butterfly functional β -diversity and regional stability across multiple European metacommunities. Although a large part of our sampling locations come from northwestern Europe compared to eastern and south-eastern regions, these results suggest that increasing functional homogenization of butterflies in many European landscapes (Ekroos et al., 2010) reduces metacommunity stability (Wang et al., 2021; Wang & Loreau, 2016) and can influence the reliable provision of ecosystem functions delivered by butterflies, such as pollination and herbivory (Badenes-Pérez et al., 2010; Rader et al., 2016). Future efforts to collect butterfly abundance data through time in other European countries that are potentially less environmentally degraded, such as in eastern and south-eastern regions are necessary to evaluate the extent to which our results remain relevant in other spatial and environmental contexts.

Spatial asynchrony of abundances or biomass among local communities can be driven by β -diversity (Wang & Loreau, 2016) or by metapopulation asynchrony (Wilcox et al., 2017). In our study, we observed that the stabilizing effect of metapopulation dynamics on spatial asynchrony was greater than the influence of different facets of β -diversity. Particularly, metapopulation asynchrony drove spatial

asynchrony with a positive indirect effect on the regional stability of butterfly abundance. In other studies, spatial asynchrony mediated by metapopulation dynamics was also pointed out as an important stabilizing factor of primary productivity (Wilcox et al., 2017) and fish stocks (Schindler et al., 2010). This implies the need of maintaining genetic diversity (Chang & Smith, 2014) as well as phenotypic and phenological differences among populations (Brans et al., 2017; Schindler et al., 2010) to enhance regional stability (de Mazancourt et al., 2013). However, much of the scientific concern about the regional diversity–stability relationship focuses on the role of species and the consequences of their loss (Catano et al., 2020; Qiao et al., 2022; Wang & Loreau, 2016; Wilcox et al., 2017). Here, we demonstrate the importance of maintaining population diversity for the stability of butterfly abundances and that its preservation cannot be underestimated. An important perspective for future research is to use more refined intraspecific trait information and genetic data to investigate the eco-evolutionary mechanisms, such as plasticity or rapid adaptation (Govaert et al., 2022), that link metapopulation asynchrony to metacommunity stability.

Another aspect of our study is that we tested the modulating role of spatial distance on the stabilizing effect of β -diversity and metapopulation asynchrony. We found that greater spatial distance between communities increased both β -diversity in its different facets and metapopulation asynchrony (Figure 2a,b), corroborating the prediction that taxonomic and functional similarity between biological communities usually decreases with spatial distance (Graco-Roza et al., 2022; Soininen et al., 2007). However, it is important to highlight that spatial distance is not a mechanism in itself (Graco-Roza et al., 2022; Soininen et al., 2007), but rather it is linked to ecological factors and processes that influence community dynamics (Soininen et al., 2007), such as dispersal limitation mediated by spatial configuration (Garcillán & Ezcurra, 2003), ecological drift (Hubbell, 2001; Vellend, 2010) and also by spatially structured environmental heterogeneity (Stein et al., 2014). In this way, the inclusion of spatial distance in SEM proved to be an effective approach to explain part of the variation in different facets of β -diversity, metapopulation asynchrony and indirectly spatial asynchrony, since this predictor reflects several ecological phenomena that are central to metacommunity theory (Soininen et al., 2007).

Although most of our sampling points were concentrated in a relatively similar climatic region in Europe, and thus we had limited power to test the influence of climate, we still found that there was spatial variation in annual precipitation, and locations with higher precipitation had lower functional α -diversity, whereas temperature positively correlated with local stability (Figure 2a) and functional α -diversity (Figure 2b). These results indicate that warmer regions are more stable, reflecting more favourable conditions for butterflies. However, it is important to bear in mind that opposing relationships can also be observed depending on the taxonomic group studied. For example, a recent study identified a negative relationship between temperature and local stability of plants (Liang et al., 2022). Moreover, the opposing effects of precipitation and temperature on butterfly α -diversity in Europe might reflect the fact that, on

average, Mediterranean climates are warmer and drier and harbour a greater variety of microhabitats, which may enhance butterfly species diversity and also functional trait diversity (Numa et al., 2016). Precipitation did not exert any influence on the different facets of β -diversity, contrasting with the results of previous studies that showed a positive effect of this climate variable on the taxonomic β -diversity of birds (Catano et al., 2020) and plants (Liang et al., 2022; Wang et al., 2021).

Although we have initially hypothesized a positive relationship between species richness and mean annual precipitation, our results were not what we expected. It is important to acknowledge that the relationships between climatic variables and butterfly species richness in Europe are complex and vary regionally depending on several factors (Stefanescu et al., 2011), such as: (i) topography; (ii) ecosystem type and (iii) land use type and intensity. For example, on the European continent, temperature is one of the main limiting factors for butterfly richness in northern regions (Luoto et al., 2006), whereas in warmer regions, such as the Mediterranean, water availability is the main limiting factor (Herrando et al., 2019; Stefanescu et al., 2011) due to recurrent precipitation deficits (EEA, 2012; Herrando et al., 2019). Thus, new studies about diversity–stability relationships across scales should ideally include variables related to climate, land use and topography in order to account for such complexities.

Theory predicts that the larger the number of local communities, the larger the probability of spatial asynchrony among those communities (Wang & Loreau, 2014). However, considering the entire dataset, the number of local communities had no influence on taxonomic β -diversity nor on spatial asynchrony. This finding is at odds with the results obtained in empirical studies that focused on birds (Catano et al., 2020) and plants (Liang et al., 2022). On the other hand, we found a negative correlation between the number of local communities and functional β -diversity, while the relationship was positive with metapopulation asynchrony. This suggests that, at least for butterflies in Europe, increasing the number of available habitat patches within regions (here 20×20km) likely results in differential responses of local populations, which consequently increases regional stability. This pattern is likely driven by different environmental conditions among sites and/or dispersal limitation among them. On the other hand, we notice that local stability was overall more important for metacommunity stability than spatial asynchrony. This might reflect the fact that only three to five locations are included in each metacommunity in our study (with each grid cell 20×20km). Thus, it might be that the relatively small area and few locations considered here result in limited climatic and environmental variation across locations, limiting our capacity to find expected functional differences in composition and thus in spatial asynchrony. It is conceivable that the significant differences in metapopulation and spatial asynchrony between low and high mobility species would be stronger if we had considered larger areas and more local communities, thus enhancing the range of environmental conditions and the potential for dispersal limitation to increase asynchronous responses among sub-populations.

4.2 | Impact of species dispersal ability on stability at multiple scales

By analysing groups of species with relatively lower and higher dispersal capacity separately within the same sampling sites and meta-communities, we found clearly distinctive patterns. First, regional stability was on average higher for more mobile species, suggesting that dispersal ability is an important process of metacommunity stability. The fact that the variability of regional abundance is higher for less mobile species might indicate that they are at higher risk of extinction due to climate change and land-use change, which are factors known to enhance population variability and population declines (Costache et al., 2021; Ekroos et al., 2010). Metacommunity theory assumes that species dispersal from the regional species pool is a central process determining both α and β -diversity (Leibold et al., 2004), but it has not been well explored in studies of metacommunity stability yet. Here, we observed that higher dispersal ability enhanced both taxonomic and functional α -diversity of European butterflies, which were both important determinants of local stability and, thus, indirectly influenced regional stability. Higher α -diversity thus explains why regional stability is higher for more mobile species compared to less mobile species. However, metapopulation asynchrony was higher for less mobile species, which positively scaled up to influence regional stability in this group, as expected. Moreover, our prediction of higher functional β -diversity for less mobile species compared to high mobile species was corroborated, although the opposite pattern was observed when we analysed taxonomic β -diversity. This seems to suggest that higher functional β -diversity is linked to dispersal limitation (but see Graco-Roza et al., 2022) in our study, affecting the distribution of the measured traits across the landscape. For instance, it seems that highly mobile species were able to effectively disperse through the landscape, but the existing environmental variation was insufficient to strongly filter species by size and egg volume. This resulted in functional homogenization of these traits across the landscapes for highly mobile species. By contrast, some small species of the low mobility group are likely strongly limited in dispersal capacity, which seems to constrain their distribution in the landscape and to enhance functional β -diversity through ecological drift (see also Chase, 2010). In the meantime, taxonomic β -diversity was higher for the group of more mobile species, suggesting that more efficient dispersal triggers effective species sorting (Gianuca et al., 2017), allowing each species to more effectively track their suitable environmental conditions when compared to relatively poor dispersers. Future studies could gain more insight into niche-based species sorting and habitat selection by integrating more traits than only wing span and egg volume, and by relating detailed environmental characteristics of the habitat patches to multi-trait β -diversity.

4.3 | Implications for biodiversity conservation

Global change and associated anthropogenic pressures on Earth, including habitat fragmentation and climate change, are leading to biodiversity erosion as well as temporal shifts in species composition

locally and regionally (Cardinale et al., 2012; Dornelas et al., 2014). This is concerning because changes in climate and connectivity can impact the local and spatial insurance provided by biodiversity, implying that more action is needed to guarantee the reliable provision of ecosystem processes and services in the Anthropocene. Our findings are particularly relevant in the context of the '30x30' goal of the Global Biodiversity Framework, which aims to conserve at least 30% of terrestrial and aquatic ecosystems through the establishment of protected areas and other effective area-based conservation measures (Waldron et al., 2020). Habitat protection and successful restoration of ecological processes can positively impact local and regional diversity (Holl et al., 2022). Our results indicate that local stability is the main driver of regional stability, suggesting that habitat protection and restoration might be important to increase both local and regional stability of butterflies. This agrees with studies that report a high contribution of local scale processes to the regional stability of multiple organisms (e.g., Wisnoski et al., 2023).

In addition to habitat protection and restoration locally, enhancing landscape connectivity by means of ecological corridors might allow species with limited dispersal capacity to track their suitable environmental and climatic conditions as they change in space (Diengdoh et al., 2023; Habel et al., 2020; Hodgson et al., 2022). High structural connectivity could, thus, potentially increase taxonomic and functional α -diversity of less mobile species, positively impacting their local and regional stability. However, some studies suggest that improving connectivity, although important, might not be sufficient to enable species to cope with rapid climate changes (Coristine et al., 2016; Fourcade et al., 2021). Thus, other management strategies, such as increasing the percentage of protected areas should also be contemplated (Rada et al., 2019). Importantly, a single large reserve might not be preferable, because for the same amount of habitat area protected, a network of several connected habitat patches covers more spatial extent and potentially also encompasses more environmental conditions. In addition, several small protected areas might be advantageous to spread and dilute extinction risk across multiple sub-populations (Fahrig, 2020). This is especially relevant for less mobile species as we demonstrate that metapopulation dynamics is an important determinant of spatial asynchrony, and therefore should be carefully considered in conservation strategies that aim at enhancing regional stability. Thus, both local and regional conservation strategies are fundamental for maintaining the provision of ecosystem services at larger scales, and for improving the resistance and resilience of ecosystems in the face of anthropogenic disturbances.

4.4 | Limitations and perspectives

Given the distribution of the plots analysed in our study, concentrated in northwestern Europe (mainly in England and the Netherlands), it is necessary to exercise some caution when interpreting our results, since the countries of eastern and southern Europe are absent or underrepresented in our analyses. It is also worth mentioning that although the sampling configuration somewhat limited the climatic

variation in space, climate still proved to be important for taxonomic and functional α -diversity (entire dataset). Thus, we suggest that future efforts should be made to collect high-quality data in other parts of Europe and the world. We believe that future diversity–stability studies that are more representative in terms of the geographical distribution of sampling points and climatic conditions on the European continent will be able to reveal an even greater relevance of climate on stability across multiple spatial scales.

5 | CONCLUSIONS

Although we observed a high redundancy between the taxonomic and functional-based approaches at the local scale, functional β -diversity was a more important driver of spatial asynchrony than its taxonomic counterpart when we focused on the entire dataset. By integrating climatic variables and spatial distance, we were able to reveal various pathways leading to regional stability. All investigated variables contributed directly and/or indirectly to the regional stability of butterfly abundance, mainly through the stability of local communities. Our study revealed consistent stabilizing effects of taxonomic and functional diversity at different scales, supporting the predictions of the local and spatial insurance hypothesis of biodiversity (Loreau et al., 2003; Yachi & Loreau, 1999). Our results indicate that the stability of metacommunities of both high and low mobility species is more influenced by local stability than by spatial asynchrony, suggesting the need to preserve or restore local habitat quality to maintain or enhance regional stability. However, compared to good dispersers, less mobile species were characterized by significantly higher metapopulation and spatial asynchrony (Figure 3e,f), as expected. Therefore, managers seeking to reduce regional variability of species with limited dispersal capacity should also take a landscape perspective into account, enhancing connectivity and the preservation of multiple sites to conserve metapopulation and meta-community dynamics.

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DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study can be accessed on Figshare at: <https://doi.org/10.6084/>

[m9.figshare.24716334](https://doi.org/10.6084/m9.figshare.24716334). These data include metrics of European butterfly stability (e.g., regional stability), geographical and climatic variables, species dispersal ability, as well as metrics of functional and taxonomic diversity at various spatial scales.

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BIOSKETCH

The team of authors is broadly interested in understanding which factors stabilize animal populations and communities at various spatial scales, highlighting the role of different facets of biodiversity, connectivity and climate on the diversity–stability relationship.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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