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CENTRO DE BIOCIÊNCIAS
CURSO DE GRADUAÇÃO EM ECOLOGIA

AVALIANDO MÚLTIPLOS FATORES DE ESTABILIDADE DA ABUNDÂNCIA DE BORBOLETAS AO LONGO DA EUROPA

Leonardo Cruz de Souza

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Monografia apresentada como parte dos requisitos para obtenção do título de Bacharel em Ecologia pela Universidade Federal do Rio Grande do Norte.

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Natal, 10 de fevereiro de 2022

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ATA DE DEFESA DE TRABALHO DE CONCLUSÃO DE CURSO DE GRADUAÇÃO

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Às 9 horas do dia 10 de fevereiro de dois mil e vinte e dois em sessão pública virtual, por meio de videoconferência meet.google.com/akh-qtke-udq, na presença da Banca Examinadora presidida pelo(a) **Professor(a) orientador(a) Andros Tarouco Gianuca** lotado(a) no Departamento de ECOLOGIA - DECOL e composta pelos examinadores: Prof. Dr. Carlos Roberto Sorensen Dutra da Fonseca e Dr. Vinícius Augusto Galvão Bastanizi, o(a) **aluno(a) Leonardo Cruz de Souza** apresentou o Trabalho de Conclusão de Curso intitulado **“*Assessing multiple drivers of stability in butterflies’ abundance across Europe*”** como requisito curricular indispensável para a integralização do Curso de Bacharelado em **Ecologia - Bacharelado - Presencial - MT**. A Banca Examinadora deliberou e decidiu pela **aprovação** do referido trabalho, com nota igual a **10 (dez)**, divulgando o resultado formalmente ao aluno e demais presentes e eu, na qualidade de Orientador(a) e Presidente da Banca, lavrei a presente ata que será assinada eletronicamente por mim, pelos demais examinadores e pelo aluno através do sistema SIPAC/UFRN.

SUMMARY

Assessing multiple drivers of stability in butterflies' abundance across Europe

Texto nos padrões da revista *Global Ecology and Biogeography*

RESUMO

As pressões antrópicas sobre os ambientes naturais têm causado perda da biodiversidade com consequências importantes para a provisão e estabilidade de serviços ecossistêmicos. No entanto, a grande maioria dos estudos sobre biodiversidade e estabilidade tem se concentrado em escalas espaciais finas e ainda não sabemos bem como os diferentes aspectos da diversidade influenciam a estabilidade do ecossistema através de escalas. Aqui, utilizamos um banco de dados de escala continental de abundâncias de borboletas (231 espécies e 349 metacomunidades) e Modelagem por Equações Estruturais (MEE) para avaliar o papel da distância geográfica, diversidade α e β na estabilização de propriedades agregadas do ecossistema (por exemplo, abundância de espécies) em múltiplas escalas espaciais ao longo da Europa. Múltiplas variáveis são importantes na rede de processos que determinam a estabilidade do ecossistema em diferentes escalas espaciais. A estabilidade da comunidade (local) aumentou com a estabilidade de espécies e a assincronia de espécies, enquanto que a estabilidade local e a assincronia espacial aumentaram a estabilidade na escala de metacomunidade (regional). A estabilidade local e a assincronia metapopulacional foram os principais fatores de estabilidade regional e assincronia espacial, respectivamente. A biodiversidade (diversidade α e β) aumentou a estabilidade ao aumentar a assincronia entre espécies, metapopulações e comunidades. A distância geográfica entre as comunidades também foi importante como um fator indireto de estabilidade regional através de seu efeito positivo na diversidade β e assincronia metapopulacional. A estabilidade regional das propriedades do ecossistema vem de vários caminhos, com implicações diretas para conservação e gestão. Além disso, nossos resultados indicam que a perda contínua de biodiversidade e a homogeneização biótica podem desestabilizar os processos ecossistêmicos através do aumento da sincronia entre espécies e comunidades locais.

PALAVRAS-CHAVE

diversidade beta, homogeneização biótica, conservação, estabilidade do ecossistema, distância geográfica, seguro local, insetos, assincronia espacial, seguro espacial, assincronia de espécies

ABSTRACT

Aim: Anthropogenic pressures on natural environments have been causing a loss of biodiversity with important consequences for the provision and stability of ecosystem services. However, the vast majority of studies on biodiversity and stability have focused on fine spatial scales and we still do not know well how different aspects of diversity influence ecosystem stability across scales. Here, we investigate the role of geographic distance, α and β-diversity in stabilizing aggregate ecosystem properties (e.g., species abundance) across spatial scales.

Location: Europe.

Time period: 2005-2016.

Major taxa studied: Butterflies.

Methods: We coupled a continental scale database of butterflies' abundances (231 species and 349 metacommunities) and Structural Equation Modeling (SEM) to evaluate the direct and indirect effects of multiple variables in stabilizing ecosystem properties across spatial scales.

Results: Multiple variables are important in the network of processes that determine ecosystem stability across spatial scales. Community (local) stability increased with species stability and species asynchrony, while local stability and spatial asynchrony increased stability at the metacommunity (regional) scale. Local stability and metapopulation asynchrony were the main drivers of regional stability and spatial asynchrony, respectively. Biodiversity (α and β-diversity) increased stability by increasing asynchrony among species, metapopulations and communities. The geographic distance among communities was also important as an indirect driver of regional stability through its positive effect on β-diversity and metapopulation asynchrony.

Main conclusions: Regional stability of ecosystem properties come from multiple pathways, with direct implications for conservation and management. In addition, our results indicate that ongoing biodiversity loss and biotic homogenization can destabilize ecosystem processes by increasing the synchrony among species and local communities.

KEYWORDS

beta diversity, biotic homogenization, conservation, ecosystem stability, geographic distance, local insurance, insects, spatial asynchrony, spatial insurance, species asynchrony

1. INTRODUCTION

There is growing evidence that maintaining biodiversity benefits ecosystem functioning by increasing its temporal stability (Bai *et al.*, 2004; Tilman *et al.*, 2006, 2014; Ptacnik *et al.*, 2008; Isbell *et al.*, 2009, 2015; Hector *et al.*, 2010; Gross *et al.*, 2014; Hallett *et al.*, 2014; Craven *et al.*, 2018). There are many overlapping mechanisms through which diversity can increase stability (Downing *et al.*, 2014; Fu *et al.*, 2019), but the most commonly found is the compensatory dynamics (increased asynchrony)(Craven *et al.*, 2018). Compensatory dynamics occurs when the temporal variation of species abundances or biomasses are negatively correlated (i.e., low species synchrony); that is, declines in some species can be compensated by increases in others and its net effect generates stability (Bai *et al.*, 2004; Hector *et al.*, 2010). Higher diversity is expected to increase the probability of asynchronous fluctuations among species (Loreau & De Mazancourt, 2008). However, the studies mentioned above come primarily from relative small-scale experiments (mainly in grasslands), although conservation strategies are normally thought regionally (rather than at the scale of a local community). Therefore, from an applied point of view, scaling up from population and community processes to ecosystem level stability is a key step in predicting the consequences of environmental changes at scales relevant to conservation and management (cf. regional or landscape scales)(Snelgrove *et al.*, 2014; Isbell *et al.*, 2017; Gonzalez *et al.*, 2020).

With the development of a recent theoretical framework, the processes that determine the temporal stability of ecosystem aggregate properties (e.g., species abundance) at multiple spatial scales can be quantified (Wang & Loreau, 2014, 2016). Following Wang and Loreau (2014, 2016), here we define stability at any given scale as the invariability of species abundances through time. From the local community perspective, local stability can result from two main processes. First, a higher average temporal stability of species (species stability) can stabilize local communities due to low temporal variation (Figure 1D). Second, asynchronous temporal responses among species (species asynchrony) can increase local stability through compensatory dynamics (Figure 1C). Likewise, higher stability at the metacommunity scale (regional stability) can result from higher temporal stability within communities (local stability, Figure 1C-D) and/or also from the degree to which local communities vary asynchronously in respect to each other (spatial asynchrony, Figure 1B). Spatial asynchrony can arise through species turnover, which reflects differences in species composition among a set of communities (i.e., spatial β-diversity). As the local communities have more dissimilar species composition, they are expected to exhibit more asynchronous responses to common environmental variation than those with higher similarity (Wang & Loreau, 2016).

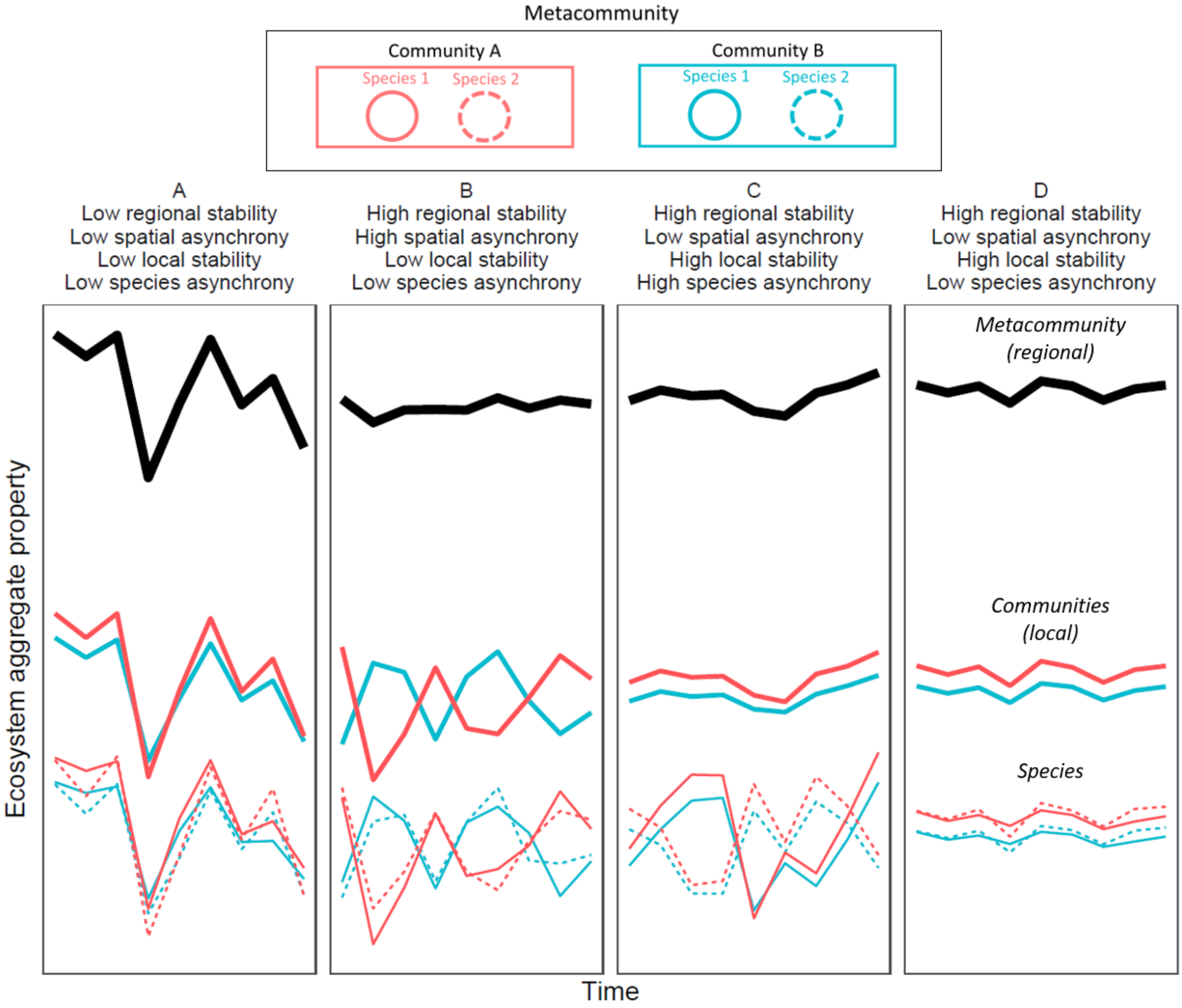

FIGURE 1 Conceptual figure illustrating how stability and asynchrony at multiple spatial scales combine to determine the regional stability of an ecosystem aggregate property (e.g., species abundance). **A)** Highly synchronous dynamics of species within and between communities results in low stability at the regional scale. **B)** Despite reduced local stability resulting from synchronized species fluctuations, local communities vary asynchronously due to the high asynchrony of the same species in different local communities, which results in a high regional stability. **C)** High species asynchrony within communities and low species-level asynchrony between communities. This results in high regional stability due to stable (and synchronous) communities. **D)** High regional stability as a result of stable (and synchronous) species and communities. Adapted from Wilcox *et al.* (2017).

Another source of spatial asynchrony, although not accounted for in this first framework, is the contribution of the metapopulation asynchrony (i.e., same species in different local communities, Figure 1B), which can also stabilize ecosystem functioning (Wilcox *et al.*, 2017). Metapopulation asynchrony can arise due to multiple factors, such as variations in environmental characteristics across local communities (Doak & Morris, 2010; Thorson *et al.*, 2014), genotypic or phenotypic differences (Schindler *et al.*, 2010; Moore *et al.*, 2014; Brans *et al.*, 2017), species interactions and demographic stochasticity (de Mazancourt *et al.*, 2013). Thus, it is also important to integrate the latter as a potential component of spatial asynchrony, along with other variables that can influence the local stability or spatial asynchrony and its components in a single causal model (Figure 2, Table 1).

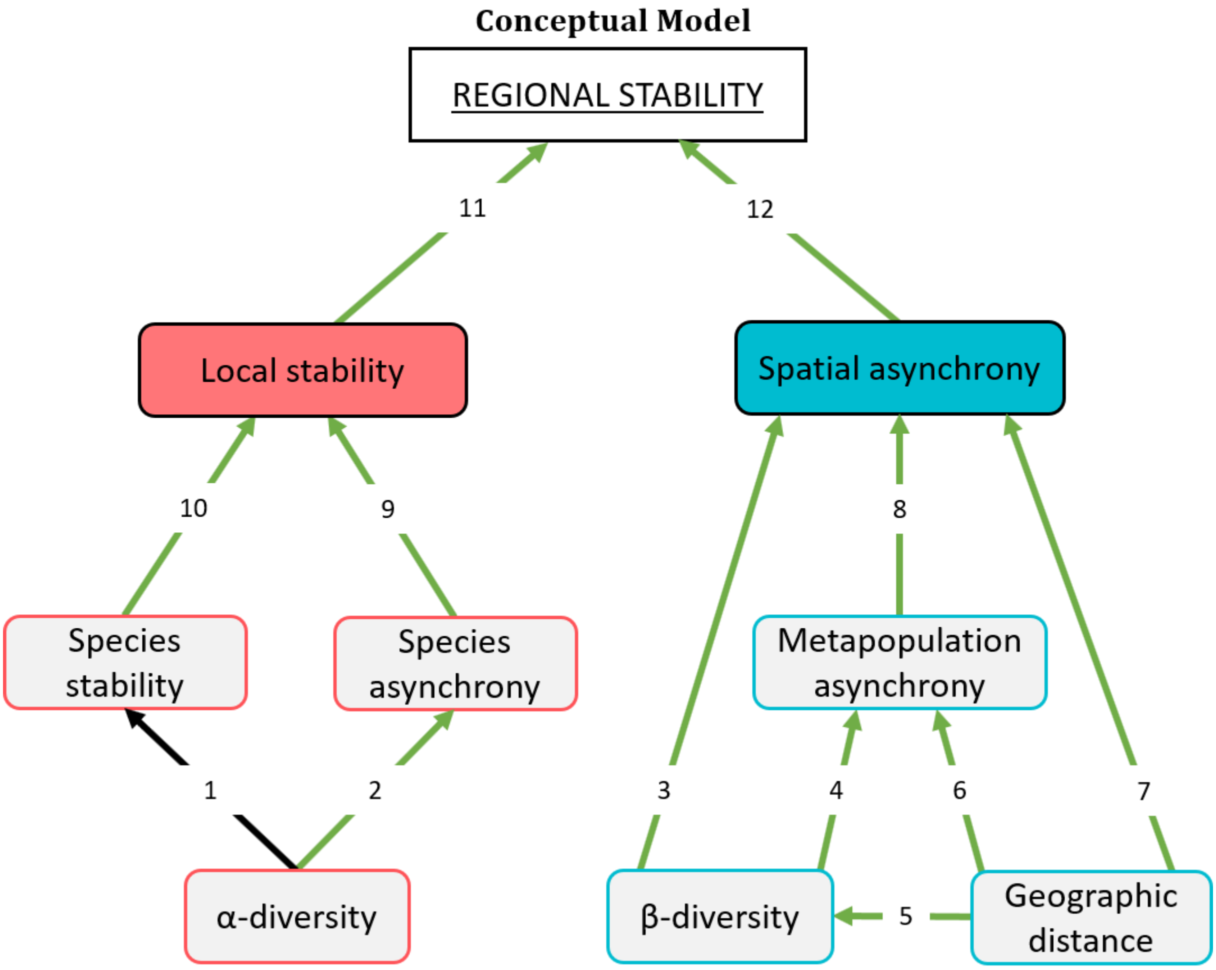

FIGURE 2 Conceptual model showing the hypothesized network of processes that can influence biodiversity, stability and asynchrony at multiple spatial scales, which ultimately determine regional stability. Red and blue boxes represent variables from within and among local communities, respectively. Green arrows indicate positive effects and the black arrow can have either a positive or negative effect. Each path is numbered and described in Table 1.

TABLE 1 Pathways, hypotheses and implications for management and conservation

Path	Hypothesis and mechanism	Implications	References
(1) α-diversity → species stability	Higher α-diversity can either increase or decrease the temporal variation of individual species abundances within a community	-	(Thibaut & Connolly, 2013)
(2) α-diversity → species asynchrony	Higher α-diversity generates greater differences in niches preferences and increases the probability of asynchronous fluctuations among species	Maintain/increase local biodiversity through conservation and restoration of habitats	(Loreau & De Mazancourt, 2008)
(3) β-diversity → spatial asynchrony	Higher dissimilarity in species composition among local communities increases the probability of asynchronous fluctuations among them	Prevent or reduce environmental and biotic homogenization	(Wang & Loreau, 2016; Wang *et al.*, 2021)
(4) β-diversity → metapopulation asynchrony	Higher dissimilarity in species composition among local communities provides a greater likelihood of distinct inter-specific interactions of the same species populations across space	See recommendation for hypothesis (3)	To be tested
(5) Geographic distance → β-diversity	Higher geographic distance among local communities can generate β-diversity through spatially structured environmental variation, demographic stochasticity and low dispersal rates	Conserve/restore distinct habitat types and/or increase the size/number of protected areas to encompass more spatially structured environmental variation	(Soininen *et al.*, 2007)
(6) Geographic distance → metapopulation asynchrony	Higher geographic distance can generate more spatially structured environmental variation and increase the likelihood of asynchronous fluctuations among same species across local communities	See recommendation for hypothesis (5)	To be tested
(7) Geographic distance → spatial asynchrony	Higher geographic distance can generate more spatially structured environmental variation and increase the likelihood of asynchronous fluctuations among local communities	See recommendation for hypothesis (5)	To be tested
(8) Metapopulation asynchrony → spatial asynchrony	Higher asynchrony of the same species in distinct local communities can contribute to spatial asynchrony	Conserve/restore species populations	(Schindler *et al.*, 2010; Wilcox *et al.*, 2017)
(9) Species asynchrony → local stability	Higher asynchrony among species within a community increases the temporal of stability of the community because declines in some species can be compensated by increases in others	See recommendations for hypothesis (2)	(Loreau & de Mazancourt, 2013; Lamy *et al.*, 2019)
(10) Species stability → local stability	Higher temporal stability of species abundances within communities increases (cascades to) local stability due to the low temporal variation in individual species abundances	-	(Thibaut & Connolly, 2013)
(11) Local stability → regional stability	Higher temporal stability of local communities cascades to the metacommunity scale	See recommendations for hypothesis (2)	(Wang & Loreau, 2014)
(12) Spatial asynchrony → regional stability	This mechanism is the scaled-up version of path (9), with communities instead of species. Higher asynchrony among local communities stabilizes ecosystem functioning because declines in some communities can be compensated by increases in others. Despite low stability in some local communities, the ecosystem function/property at the metacommunity scale is maintained	See recommendations for hypothesis (3), (5) and (8)	(Wang & Loreau, 2014)

Within a spatial context, the geographic distance among local communities can influence regional stability as it encompasses a set of processes, such as spatially structured environmental variation, demographic stochasticity and dispersal (Xue *et al.*, 2014; Fluck *et al.*, 2020; Zeni *et al.*, 2020). In the distance decay relationship (Soininen *et al.*, 2007), biological similarity decreases with geographical distance (i.e., the spatial β-diversity increases). This relationship can be driven by three main processes, which are not mutually exclusive: (i) decreasing similarity in environmental characteristics with distance can result in species sorting, and thus higher β-diversity (Zellweger *et al.*, 2017); (ii) spatial configuration of the landscape influence the dispersal rate of organisms — for example, topographic heterogeneity leads to a higher decrease in similarity with distance (Garcillán & Ezcurra, 2003); (iii) according to neutral theory (Hubbell, 2001), ecological drift, random dispersal and random speciation can result in community similarity decays with increasing geographic distance, even in homogeneous environments. Furthermore, dispersal can also influence regional stability by maintaining local and regional diversity as it allows species to track suitable environmental conditions (Stuhldreher & Fartmann, 2014) and promote species coexistence (Loreau *et al.*, 2003; Shanafelt *et al.*, 2015).

To investigate drivers of stability across scales, we focused here on insects, which is a major and important group of organisms, comprising over half of the world's multicellular terrestrial species (Stork, 2018). In addition, insects play a vital role in ecosystem functioning and services (Noriega *et al.*, 2018; Schowalter *et al.*, 2018). For example, insects integrate food webs by linking primary producers and consumers, as well as higher-level consumers. Insects, such as butterflies, are estimated to pollinate over 80% of flowering plants (Ollerton *et al.*, 2011; Vanbergen *et al.*, 2013), strongly contributing to the primary productivity of many ecosystems, being particularly important to agriculture (Klein *et al.*, 2006; Vanbergen *et al.*, 2013). They also provide many other ecosystem services upon which humans depend, including medical and industrial products, biological control, decomposition, nutrient cycling, among others (Noriega *et al.*, 2018; Schowalter *et al.*, 2018). The ecological services provided by insects was evaluated to be at least $57 billion in the United States annually (Losey & Vaughan, 2006), with recent estimates suggesting that crop pollination by insects supports $361 billion of crop production worldwide (Lautenbach *et al.*, 2012).

More recently, there has been growing attention on the global insect declines (Cardoso *et al.*, 2020; Wagner, 2020; Wagner *et al.*, 2021). The current knowledge about this group is still incipient (Stork, 2018), but a meta-analysis revealed that 40% of insect species are threatened with extinction (Sánchez-Bayo & Wyckhuys, 2019), with Lepidoptera, Hymenoptera and Coleoptera being the most affected. Among the main drivers of extinctions, habitat loss due to land conversion for agriculture appears first (Sánchez-Bayo & Wyckhuys, 2019), followed by other factors, such as urbanization, pollution, invasive species and climate change (Cardoso *et al.*, 2020; Piano *et al.*, 2020). Thus, severe insect declines might have global ecological and economic consequences and it is important to better understand what factors increase the stability of insect populations under scenarios of global change.

Butterflies are well documented, popular, sensitive to disturbances and, most importantly, have a monitoring scheme in Europe (butterfly-monitoring.net). Because of these characteristics, they are a valuable environmental indicator and can also be an adequate model for many terrestrial insect groups (Thomas, 2005). In the same way as other insects, the butterflies are also experiencing an alarming global decline in their populations (Melero *et al.*, 2016; Habel *et al.*, 2019; Warren *et al.*, 2021), even in protected areas (Rada *et al.*, 2019). Therefore, understanding the mechanisms that influence the stability of this group at multiple spatial scales can also help as an overall guide for insects' conservation, for which data is scarce.

Here, we use a continental-scale butterfly abundance database to assess the role of geographic distance, α and β-diversity on the stability and asynchrony components of regional stability in 349 metacommunities across Europe. This database provides a great opportunity to test the theory and understand what processes stabilize ecosystem properties in a wide range of environments and scales. We used a structural equation modeling approach to quantify the direct and indirect effects of geographic distance, α and β-diversity in stabilizing regional ecosystem properties across multiple spatial scales.

2. MATERIALS AND METHODS

2.1 Database

The database comes from the long-term citizen science European Butterfly Monitoring Scheme (eBMS). The raw database included 8568 unique transect sections (see below) *ca.* 200 m long (mean ± SD = 203 ± 11), spanning from 1990 to 2016, from the butterfly monitoring scheme of nine countries: Spain, France, Germany, Luxembourg, Belgium, Netherlands, United Kingdom, Sweden and Finland (Figure S1). All the monitoring schemes are based on Pollard-walk transects (Pollard, 1977; Van Swaay *et al.*, 2015). Usually, during the butterflies' flight season (March-April and September-October) and when weather conditions meet specified criteria, volunteers count all individual butterflies detected along a fixed transect route divided into smaller sections. The volunteers count all butterflies in an imaginary box 2.5 m to their sides and 5 m ahead and above them. As the volunteers cannot detect all the butterflies in a transect, transect counts provide estimates of species-specific abundance rather than absolute values. For each transect section, the abundance of each species is summed yearly and reflects year-to-year population changes. Most of the transects are monitored by skilled volunteers and the counts are reported annually to build long-term time series. For the detailed eBMS methodology see Van Swaay *et al.* (2012, 2015) and Sevilleja *et al.* (2019).

Because transects are divided into smaller sections, some subdivisions of the same transect had equal geographic coordinates (i.e., overlapped points in the map). To overcome this issue, we added a 200 meters buffer separating the transect sections based on their section number. For example, consider 4 subdivisions of the same transect “T” (T_1, T_2, T_3 and T_4), all with the same coordinates. First, the direction is chosen at random (north, south, east or west) and then the last three are separated from the first by 200, 400 and 600 meters, respectively. This procedure was done in 1034 of the 4387 transect sections before delimiting the metacommunities and sampling (see next section).

2.2 Data selection

First, we selected only transect sections between the years of 2005 and 2016, which was the temporal window for most of the data and countries. Second, only transect sections that were revisited three or more months per year (5 ± 1) were used. Each transect section was considered a local community, and a set of these, which could vary between three to five (to even the sampling effort between countries), a metacommunity. To delimit a metacommunity, a grid with cells of 20 × 20 kilometers was plotted over a map of Europe, resulting in 349 metacommunities (Figure 3). In case a metacommunity was composed of more than five local communities, three, four or five were randomly sampled. Because the countries started the monitoring scheme in different years, the monitoring time among metacommunities could vary between four and twelve consecutive years (8.9 ± 2.7), but all local communities within each metacommunity had the same consecutive monitoring time.

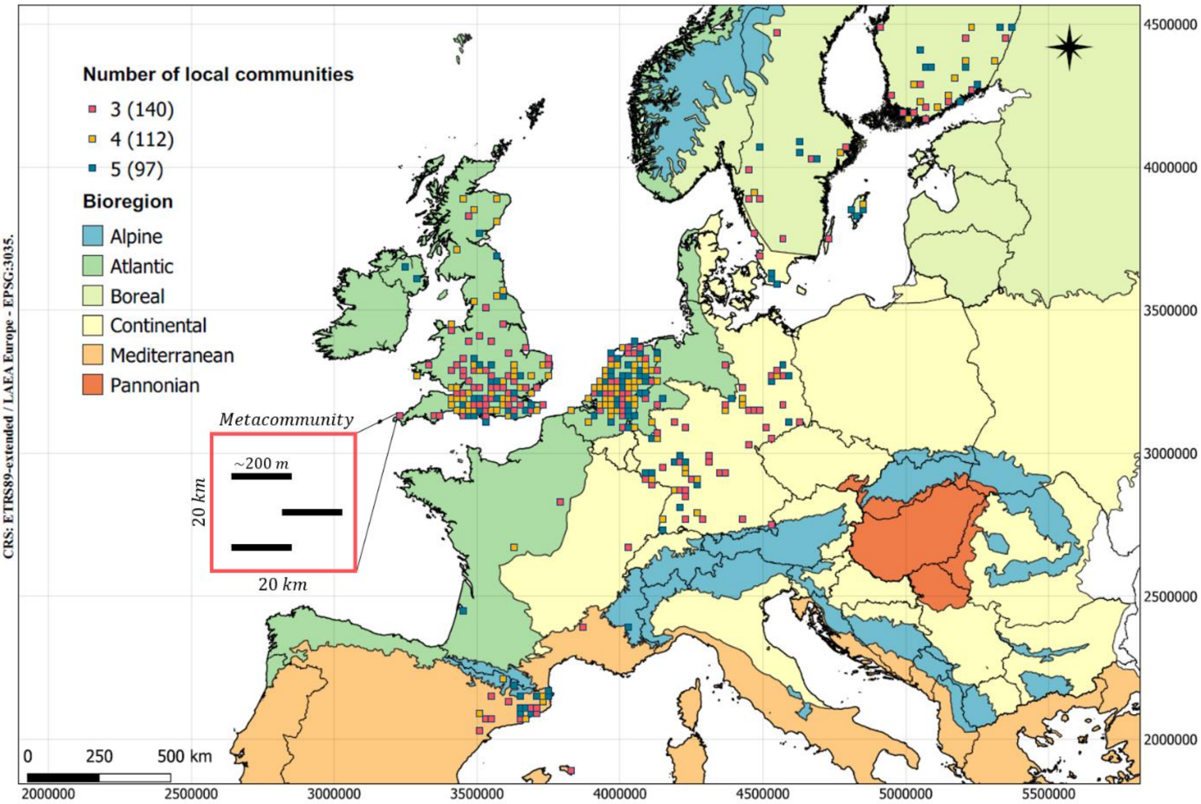

FIGURE 3 Map showing the distribution of the 349 butterfly metacommunities across Europe. Red, yellow and blue squares represent metacommunities with three, four and five local communities, respectively. Numbers in parentheses are the frequency of each class. The metacommunities boundaries were defined by plotting a grid with cells of 20 x 20 kilometers over the map of Europe. All transect sections (*ca.* 200 m long) within each grid cell were considered part of that metacommunity. In case a metacommunity had more than five local communities, three, four or five were randomly sampled.

2.3 Calculation of stability components

For each metacommunity (i.e., grid cell), species abundance was used to calculate regional stability and its components (Table 2), following (Loreau & De Mazancourt, 2008; Wang & Loreau, 2014). Here, the variability and synchrony metrics were inverted to represent stability and asynchrony, respectively. All calculations were performed in the R software environment (R Core Team, 2021) adapting the code available in Wilcox *et al.* (2017). The formulas used to calculate each metric are presented below, as follows:

Regional stability (R_{stb}),

$$R_{stb} = \frac{\mu_M}{\sigma_M} \quad (1)$$

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

Spatial asynchrony (φ),

$$\varphi = \left(\frac{\sum_{i,j} w_{ij}}{\left(\sum_i \sqrt{w_{ii}}\right)^2} \right)^{-1} \tag{2}$$

where w_{ij} is the temporal covariance between communities i and j, and w_{ii} is the temporal variance of community i, as referenced from a covariance matrix.

Metapopulation asynchrony (φ_{mpop}),

$$\varphi_{mpop,i} = \left(\frac{\sum_{m,n} w_{mn}}{\left(\sum_m \sqrt{w_{mm}}\right)^2} \right)^{-1} \tag{3}$$

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.

TABLE 2 Descriptions of ecosystem stability metrics (adapted from Wilcox *et al.* 2017)

Name	Symbol	Short description	Ecological description
Regional stability	R_{stb}	Temporal invariability of the total metacommunity abundance	Ecosystem stability at the metacommunity scale
Spatial asynchrony	φ	The degree to which local communities' abundances vary asynchronously in respect to each other within a metacommunity through time	How much different the local communities vary from year to year in respect to each other
Metapopulation Asynchrony	φ_{mpop}	The degree of asynchrony among same species population abundances in distinct local communities within a metacommunity through time. Averaged across species to obtain a single value per metacommunity	How much different the same species populations vary in respect to each other across local communities through time
Local stability	L_{stb}	Temporal invariability of the total community abundance. Averaged across local communities to obtain a single value per metacommunity	Ecosystem stability at the local community scale
Species asynchrony	φ_{sp}	The degree of asynchrony among species abundances within a local community through time. Averaged across local communities to obtain a single value per metacommunity	How much different are species responses to environmental fluctuations from year to year
Species stability	Sp_{stb}	Temporal invariability of single species abundance. Averaged across all species and local communities to obtain a single value per metacommunity	How much stable are species-level abundances through time

Local stability (L_{stb}),

$$L_{stb} = \left(\sum_i \frac{\mu_i}{\mu_M} \times \frac{\sigma_i}{\mu_i} \right)^{-1}$$

(4)

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. This metric is averaged across all local communities, weighted by each community's total abundance, to obtain a single value for each metacommunity.

Species asynchrony (φ_{sp}),

$$\varphi_{sp,i} = \left(\frac{\sum_{k,l} w_{kl,i}}{\left(\sum_k \sqrt{w_{kk,i}}\right)^2} \right)^{-1}$$

(5)

where w is the temporal covariance matrix comparing abundances of species k and l within community i. To obtain a single value for each metacommunity, species asynchrony is averaged across communities, weighted by the total abundance of each community.

Species stability (Sp_{stb}),

$$Sp_{stb,i} = \left(\sum_j \frac{\mu_{j(i)}}{\mu_i} \times \frac{\sigma_{j(i)}}{\mu_{j(i)}} \right)^{-1}$$

(6)

where $\mu_{j(i)}$ is the mean of species j's abundance through time in community i, μ_i is the mean total abundance in community i, $\mu_{j(i)}$ is the mean abundance of species j in community i, and $\sigma_{j(i)}$ is the temporal standard deviation of species j in community i. This metric is averaged across communities, weighted by each species' relative abundance and then by total community abundance to obtain a single value for each metacommunity.

2.4 Calculating biodiversity

To estimate α-diversity, the inverse of the Simpson's index (D) was used:

$$D = \frac{1}{\sum_{i=1}^{S} p_i^2}$$

(7)

where p_i is the relative abundance of species i and S is the number of species in the local community. This metric was calculated for each local community in each metacommunity and for each year separately and then averaged. The species richness (total number of species = 231, 14 ± 6) and Shannon's diversity were also calculated, but as all the three metrics were correlated (Table S1), we opted for the inverse of the Simpson's index because it is not sensitive to sample size. The inverse of the Simpson's index was calculated using the "diversity()" function from the "vegan" package.

We used the index of Bray-Curtis ("bray.part()" function, "betapart" package) to calculate spatial β-diversity among communities for each metacommunity. The mean of the pairwise β-diversity among local communities was calculated for each metacommunity in each year separately and then averaged. We also checked for correlations between β-diversity and local diversity indices, which revealed a non-significant correlation between our measure of β-diversity and the inverse of the Simpson's index (Table S1).

2.5 Calculating geographic distance

To obtain a single value of geographic distance per metacommunity, we used the mean of the pairwise Euclidean distance between all local communities within each metacommunity. This metric was calculated using the geographic coordinates (decimal degrees, unit in meters) of each local community.

2.6 Statistical analyses

All the variables were log-transformed to normalize the residual of the linear models (except the number of local communities) and to remove the skewness of the geographic distance variable (Figure S2). In our study, the number of local communities was not constant across metacommunities. To remove any potential effect of this unevenness over the other variables, and also to avoid adding it as a covariate, we did a linear regression of them against the number of local communities and then used the residuals for all further analyses.

To evaluate multiple hypotheses from theories (Figure 2, Table 1), and the direct and indirect effects, multivariate analysis was carried out in the form of Structural Equation Modeling (SEM) using the 'piecewiseSEM' package (Lefcheck, 2016). Structural equation models combine multiple predictor and response variables in a single causal network. They are commonly represented using path diagrams (as in Figure 2), where arrows indicate directional causal relationships between observed variables. The predictor variable is from where the arrow starts and the response variable is where the arrow ends. The presumed relationships can be translated into a series of structured mathematical equations that correspond to the pathways in the model. The model is conceptualized beforehand and can be based on prior observations, experimentation and theories. Because variables can be both predictors and responses, SEM can quantify the direct and indirect (cascading) effects in a model. Our initial model (Figure 2) had a poor fit to the data (Fisher's C = 164.471 and P = 0) and the paths 1 and 7 were not significant (p-values = 0.69 and 0.14, respectively). Built in the 'piecewiseSEM' package, there is a directed separation test (Lefcheck, 2016), which provides information (a posteriori) of unrecognized significant pathways that is supported by the data. Almost all the unrecognized significant pathways (7 out of 8) were treated as correlated errors (Lefcheck, 2016). Correlated errors reflect the situation when two variables appear to be correlated but they are not presumed to have any causal relationship. Such correlations could be caused by some unmeasured variable. We added the new path (α-diversity to spatial asynchrony) and removed nonsignificant ones only if it improved model AIC, which resulted in the exclusion of path 1 (ΔAIC = 5.69). Lastly, note that in the results the variance of regional stability was fully explained because log-transforming made local stability (L_{stb}) and spatial asynchrony (φ) sum up to regional stability (R_{stb}); that is, $log_e(R_{stb}) = log_e(L_{stb}) + log_e(\varphi)$ (as in Hautier *et al.* 2020 and Wang *et al.* 2021). We checked for residual spatial autocorrelation in our SEM model by calculating Moran's *I* and there was none (Table S2).

To assess the relative importance of local stability and spatial asynchrony to regional stability, a variance partitioning was done ("varpart()" function, "vegan" package). This analysis is based on partial regressions and allows the quantification of the unique and shared contribution of a set of explanatory variables. This contribution is expressed in the form of coefficients of determination (R^2), which are estimates of how much variation in the response variable has been explained by a given component.

3. RESULTS

The final model (Fisher's C = 21.43, df = 28 and P = 0.80) explained 100%, 98% and 43% of the variance in regional stability, local stability and spatial asynchrony, respectively (Figure 4). Both local stability (standardized (std.) effect = 0.77, p < 0.001) and spatial asynchrony (std. effect = 0.45, p < 0.001) highly contributed to the increase of regional stability. Spatial asynchrony increased with β-diversity (std. effect = 0.10, p = 0.03) and metapopulation asynchrony (std. effect = 0.56, p < 0.001), and was indirectly increased by β-diversity (std.

indirect effect (0.30 × 0.56) = 0.16) and geographic distance (std. indirect effect (0.19 × 0.56) = 0.10) through metapopulation asynchrony. Spatial asynchrony decreased with α-diversity (std. effect = – 0.11, p = 0.004). Metapopulation asynchrony increased with β-diversity (std. effect = 0.30, p < 0.001) and geographic distance (std. effect = 0.19, p < 0.001), and was indirectly increased by geographic distance (std. indirect effect (0.51 × 0.30) = 0.15) through β-diversity. Local stability increased with species stability (std. effect = 0.70, p < 0.001) and species asynchrony (std. effect = 0.74, p < 0.001), and was indirectly increased by α-diversity (std. indirect effect (0.28 × 0.74) = 0.20) through species asynchrony. β-diversity increased with geographic distance (std. effect = 0.51, p < 0.001). Species asynchrony increased with α-diversity (std. effect = 0.28, p < 0.001). There was no influence of geographic distance on spatial asynchrony (std. effect = 0.07, p = 0.10) within this model.

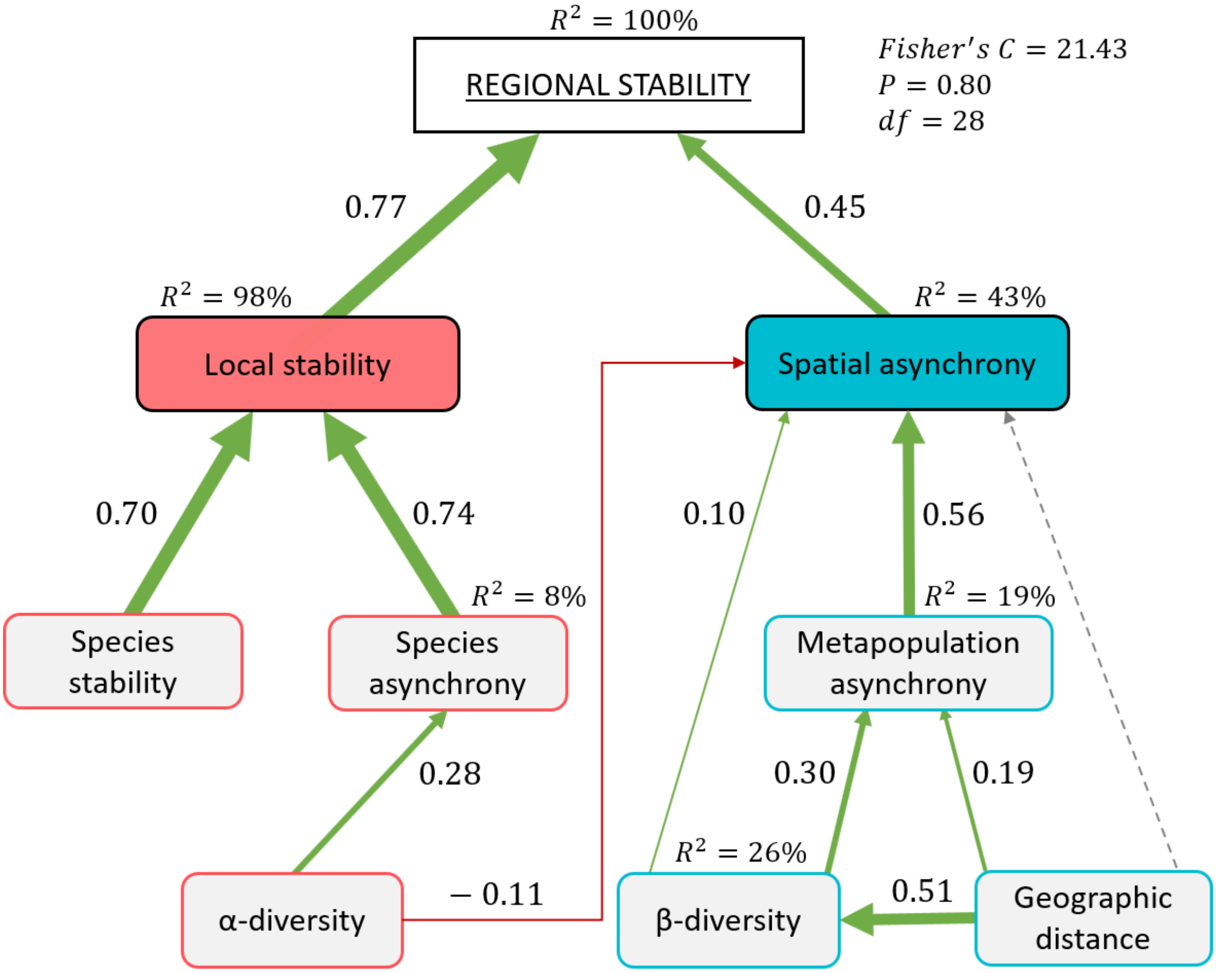

FIGURE 4 Structural equation model showing the direct and indirect pathways through which biodiversity (α and β-diversity) and geographic distance influence asynchrony and stability at multiple spatial scales. Red and blue boxes represent variables from within and among local communities, respectively. Numbers next to arrows are standardized path coefficients. Solid green arrows represent significant paths, the solid red and dashed gray arrow represent negative and nonsignificant paths, respectively. Width of paths are scaled by path coefficients.

The tests of directed separation are presented in Table 3. The critical value represents the magnitude and direction of the correlation (i.e., positive or negative). All of the new paths were treated as correlated errors (CE), with only one exception (*). The negative effect of α-diversity on spatial asynchrony was theoretically expected (Wang & Loreau, 2016).

TABLE 3 Tests of directed separation (unrecognized pathways)

Response	Predictor	Critical value	p-value
Spatial asynchrony CE	Species asynchrony	3.44	< 0.001
Spatial asynchrony CE	Species stability	3.38	< 0.001
Spatial asynchrony *	α-diversity	- 2.86	0.004
Metapopulation asynchrony CE	Species asynchrony	4.21	< 0.001
Metapopulation asynchrony CE	Species stability	4.22	< 0.001
Local stability CE	β-diversity	- 3.02	0.002
Species stability CE	β-diversity	- 6.23	< 0.001
Species asynchrony CE	β-diversity	2.61	0.009

In the variance partitioning, 100% of the variance in regional stability was explained by local stability alone (55%), spatial asynchrony alone (19%) and their shared effect (26%) (Figure 5).

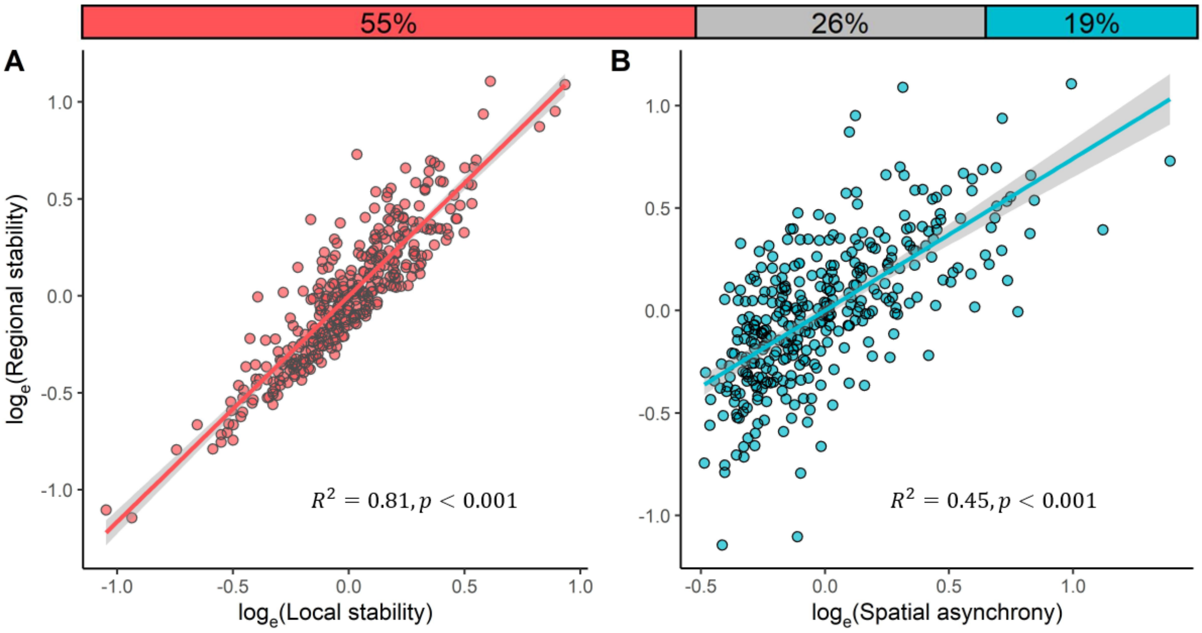

FIGURE 5 Relative importance of local stability and spatial asynchrony to regional stability in 349 butterfly metacommunities across Europe. Percentages are the variation of regional stability explained by local stability alone (red), spatial asynchrony alone (blue) and their shared effect (gray). Plots show the bivariate linear regressions (unique + shared effect) between regional stability and local stability **(A)** and spatial asynchrony **(B)**. Note that because we controlled for the number of local communities there are positive and negative values (the residuals).

4. DISCUSSION

Understanding scale-dependent effects of biodiversity on the stability of ecosystems is key to mitigate global change impacts on the delivery of ecosystem functions and services. Here we provide a synthetic overview of which processes are contributing to the stability of butterflies' abundances at multiple spatial scales across Europe. Multiple components were important in the network of processes that determine regional stability. At the local community, stability increased with both species stability and species asynchrony, while local stability and spatial asynchrony increased stability at the metacommunity scale. The contribution of biodiversity (α and β-diversity) to stability was determined by increasing asynchrony among species, metapopulations and local communities. The geographic distance among local communities was also important as an indirect driver of regional stability, especially through its positive effect on β-diversity. The results indicate that ecosystem stability at the regional scale comes from multiple pathways, with direct implications for conservation and management (see Table 1 in introduction).

We found that local stability had a stronger stabilizing effect on regional stability than spatial asynchrony (Figure 5). This finding is in agreement with some previous studies in which local stability was the primary force contributing to regional stability (Wilcox *et al.*, 2017; Lamy *et al.*, 2019; Wang *et al.*, 2019, 2021; Hautier *et al.*, 2020; all studied plants), but it is at odds with other studies where the effect of spatial asynchrony was stronger (Thorson *et al.*, 2018; Catano *et al.*, 2020; Hammond *et al.*, 2020; marine fishes, birds and coastal rock pool organisms, respectively). One possible explanation for these contrasting patterns could be the type of organisms (plants vs animals), in which local stability might be the most common mechanism stabilizing metacommunities of plants whereas spatial asynchrony seems to be the main driver of animal metacommunities. For example, the national stability of food production was found to be mainly driven by the average stability of individual crop yields rather than asynchrony among them (Mahaut *et al.*, 2021). Nonetheless, further research with other organisms, especially a multi-trophic approach (e.g., Firkowski *et al.*, 2021), will be needed for a better understanding of the underlying processes and how their relative importance varies between regions, spatial scales and organism groups.

At the local scale, species stability and asynchrony increased local stability with similar magnitudes. This finding shows that stable species can be as important to local stabilization as compensatory dynamics (see also, Grman *et al.* 2010, Sasaki & Lauenroth, 2011). As in Hautier *et al.* (2020), we did not find a relationship between α-diversity and species stability. Yet, more diverse communities increased local stability through higher asynchrony among species. As different species have different biotic and abiotic preferences, communities with higher α-diversity are more likely to present such asynchronous dynamics as the environment fluctuates (Loreau & De Mazancourt, 2008). Such results are in agreement with previous studies (Bai *et al.*, 2004; Hector *et al.*, 2010; Wilcox *et al.*, 2017; Hautier *et al.*, 2020), but here we demonstrate how such local scale dynamics scale up to impact stability at larger spatial scales.

Moreover, we also found that α-diversity had a negative effect over regional stability by decreasing spatial asynchrony, but an overall positive effect. The negative effect of α-diversity on spatial asynchrony was theoretically expected (Wang & Loreau, 2016), and could be due to high environmental correlation among local communities, as most of the sampling sites used in our study are spatially close (Figure S2). Also, this negative effect could reflect high between-species environmental correlation, as many butterfly species are very sensitive to environmental disturbances (Thomas, 2005; Whitworth *et al.*, 2018). Thus, as the different species have similar responses to environmental variation and the local communities are environmentally correlated, greater diversity is expected to strengthen the spatial synchronous responses.

When moving to the metacommunity scale, spatial variation in biodiversity and geographic distance appear as main drivers of spatial asynchrony, which supports theoretical predictions (Wang & Loreau, 2014, 2016). Regarding β-diversity, we confirm the expectations of higher asynchrony among communities with different species compositions and its stabilizing effect through spatial asynchrony (Wang & Loreau, 2016). Yet, we demonstrate that β-diversity can also increase metapopulation asynchrony. This pattern may reflect that different biotic interactions across communities owing to high β-diversity leads to compensatory responses of the same species across communities (i.e., metapopulation asynchrony). Also, the spatial asynchrony in butterflies' abundances is probably linked to the asynchrony of resource availability (host/nectar plants) in both space and time. In accordance with Wang *et al.* (2021), our results suggest that biotic homogenization can destabilize ecosystems by increasing synchrony among local communities. Below we discuss how metapopulation asynchrony and geographic distance contributed to regional stability.

Our results show that metapopulation asynchrony was the main driver of spatial asynchrony. The observed asynchronous metapopulation responses were influenced by two variables: β-diversity and geographic distance. The contribution of β-diversity could be a result of the same species varying asynchronously due to different species interactions occurring across local communities. In turn, the effect of geographic distance could reflect abiotic variations in the landscape, which is driving the populations of the same species to vary asynchronously (Doak & Morris, 2010; Thorson *et al.*, 2014). In other studies, this type of spatial asynchrony mediated by metapopulation dynamics was also claimed to be an important factor stabilizing primary productivity (Wilcox *et al.*, 2017) and fish stocks (Schindler *et al.*, 2010). If this is a common pattern, population extinctions, which were estimated to be three times greater than species extinctions rates (Hughes *et al.*, 1997), represent an underlooked threat to ecosystem stability and food supply.

Although we cannot distinguish among concurrent mechanisms, this was the first study to show how the geographic distance among communities can influence ecosystem stability at larger scales. Greater geographic distance among communities increased both β-diversity and metapopulation asynchrony. Because we did not measure abiotic variables (e.g., temperature, precipitation), the influence of geographic distance most likely represents the shared effect between environmental variables and space itself (Qian & Shimono, 2012; Chen *et al.*, 2020), such as dispersal limitation, abiotic variations and stochastic processes (Ford & Roberts, 2020). Furthermore, when considering the scenario of high spatial connectivity (i.e., low geographic distance), in which variation in environmental characteristics is minimum, we can speculate that the observed low β-diversity and metapopulation asynchrony (Figure 6) may be related to competitive exclusion (Loreau *et al.*, 2003; Shanafelt *et al.*, 2015), which reduced species turnover (Deane *et al.*, 2017) and, consequently, potential distinct interspecific interactions across space. In the spatial insurance hypothesis, Loreau *et al.* (2003) states that at high dispersal rates (high spatial connectivity in our case) the metacommunity functions as a single local community, and species that have the highest fitness for average conditions are expected to become dominant in the whole metacommunity, potentially leading to the exclusion of inferior competitors.

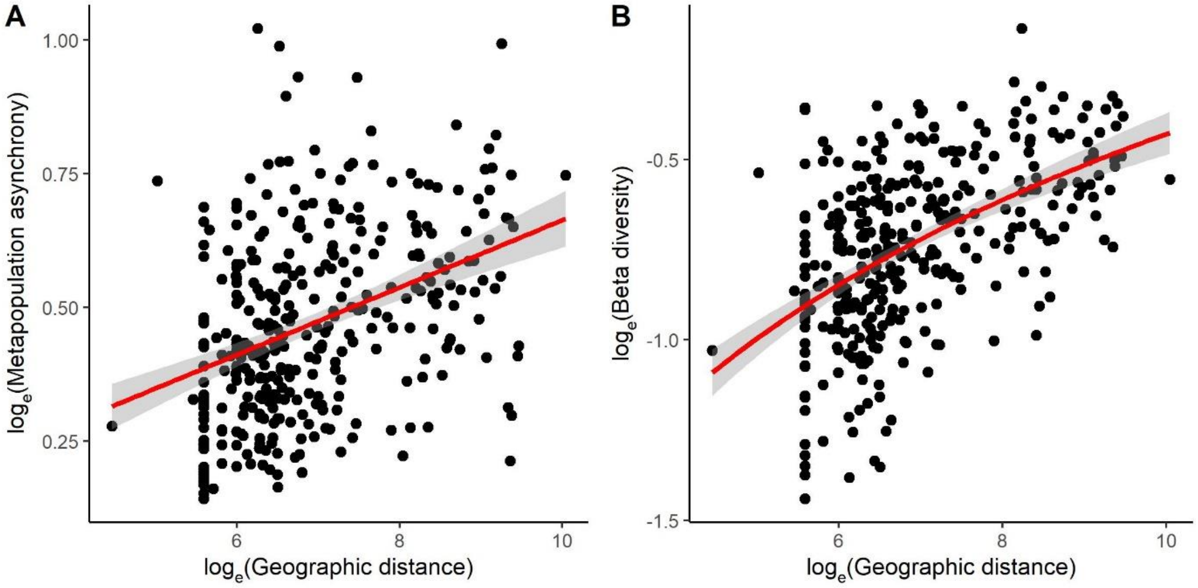

FIGURE 6 Bivariate plots showing the influence of geographic distance on **A)** metapopulation asynchrony (linear effect, $R^2 = 0.15$ and $p < 0.001$) and **B)** β-diversity (nonlinear effect, logarithmic curve). Because a logarithmic curve was fitted, we did not control for the number of local communities.

Ongoing anthropogenic activities have direct impacts over biodiversity and the environment, which can negatively affect regional stability by increasing the synchrony among species and local communities. Habitat loss/degradation decreases insects α-diversity (Fonseca, 2009; Sánchez-Bayo & Wyckhuys, 2019; Uhl *et al.*, 2021) and consequently the species asynchrony within communities, which in turn reduces regional stability by lowering local stability. This is particularly relevant for butterflies, as local stability is the main driver of regional stability. It also implies that preserving the quality of local habitats is very important and effective for this group, and probably for other insects. For example, Piano *et al.* (2020) showed that increased urbanization causes declines in insects' diversity and abundance, with 85% reduced abundance in butterflies, possibly due to the Urban Heat Island effect (Merckx *et al.*, 2018) and degradation of remaining habitats (McKinney, 2008). Biodiversity changes due to biotic homogenization, that is, reduced species turnover across space (low β-diversity; Magurran *et al.*, 2015; Blowes *et al.*, 2019), can have a double negative effect over regional stability by reducing metapopulation and spatial asynchrony. Furthermore, and particularly for mobile species, we anticipate that habitat fragmentation might decrease regional stability through reduced patch dynamics (e.g., source-sink) and by not allowing species to track suitable environments. The latter is especially relevant to species that depend on different habitat types throughout their life-cycle, such as butterflies (Eichel & Fartmann, 2008). Still, the connectivity between metacommunities becomes increasingly more relevant as some species distributions are shifting northwards due to the rapid global warming (Devictor *et al.*, 2012; Platts *et al.*, 2019), that is, without connectivity, non-thermophilic species lag behind.

Here we presented an overview of multiple drivers of stability in European butterflies' abundance across scales. In summary, α-diversity increases local stability by increasing species asynchrony and β-diversity increases spatial asynchrony through asynchrony among communities and metapopulations. Metapopulation asynchrony was the main driver of spatial asynchrony of butterflies in Europe, calling attention to the importance of intra-specific diversity. The geographic distance among communities increased β-diversity and metapopulation asynchrony. Local stability had a stronger contribution to regional stability than spatial asynchrony, implying that preserving local habitats is paramount for butterflies and probably for other insects. Lastly, the results indicate that multiple components should be preserved to ensure larger scale ecosystem stability and that the ongoing biodiversity losses and changes can reduce local and regional stability by increasing the synchrony of its components.

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6. SUPPLEMENTAL INFORMATION

Supplemental information for

Assessing multiple drivers of stability in butterflies' abundance across Europe

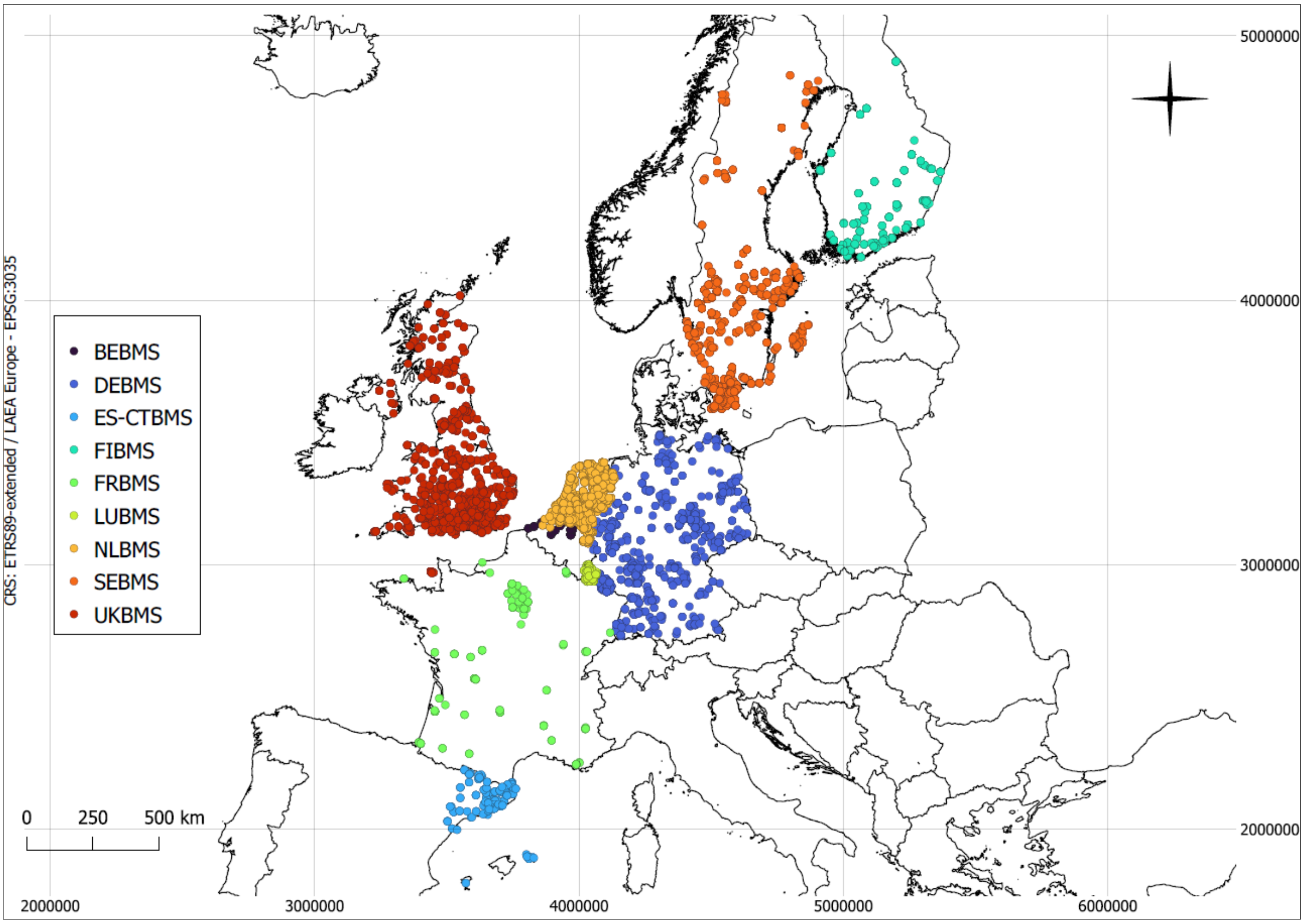

Figure S1. Distribution map of the transect sections of the raw database.

Table S1. Pearson's product-moment correlation between diversity indices. The correlation coefficients and p-values are below and above the main diagonal, respectively.

Richness	< 0.001	< 0.001	0.004
0.85	**Inverse Simpson's**	< 0.001	0.22
0.91	0.97	**Shannon's**	0.03
- 0.15	- 0.07	- 0.11	**β-diversity**

Table S2. Tests of residual spatial autocorrelation in all linear models that compose the SEM. The null hypothesis is that there is no spatial autocorrelation in the models (so we want a high p-value). The Moran's *I* was calculated using the code available in Tallavaara *et al.* (2018).

Model	Moran's *I*				
	Observed	Expected	SD	p-value	Effective N
Regional stability	- 0.009	- 0.002	0.04	0.88	349
Spatial asynchrony	0.006	- 0.002	0.04	0.83	349
Metapopulation asynchrony	0.0007	- 0.002	0.04	0.93	349
Beta diversity	0.034	- 0.002	0.04	0.40	349
Local stability	0.010	- 0.002	0.04	0.76	349
Species asynchrony	0.048	- 0.002	0.04	0.25	349

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Tallavaara, M., Eronen, J.T. & Luoto, M. (2018) Productivity, biodiversity, and pathogens influence the global hunter-gatherer population density. *Proceedings of the National Academy of Sciences of the United States of America*, **115**, 1232–1237.

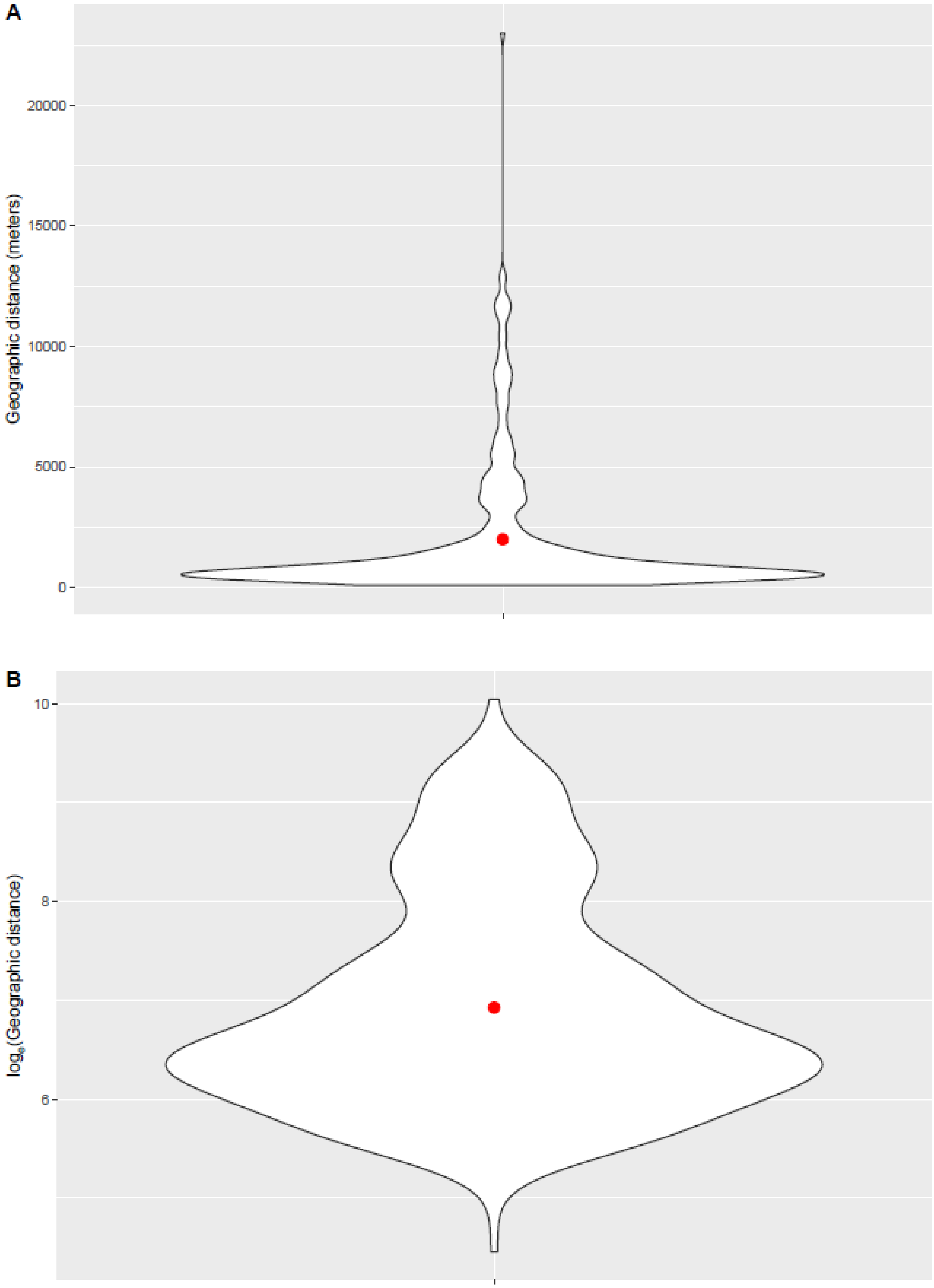

Figure S2 Violin charts of the average pairwise Euclidean distance among all local communities within each metacommunity. The red dots represent the mean.