Landscape anthropization drives composition and diversity of butterfly communities at a regional scale

Baptiste Bongibault[1*], Laurent Godet[2,] Régis Morel[3], Pierre-Yves Pasco[3], Ivan Bernez[1], et Loïs Morel[1,2,3]

[1]UMR DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, INRAE, Ifremer, Rennes, France

[2] UMR 6554 LETG, CNRS, Nantes Université, Nantes, France

[3]Bretagne Vivante, Brest, France

*corresponding author: b.bongibault@free.fr

Abstract

Aim

While landscape anthropization is a key driver of biodiversity change, its effects on communities are underexplored, especially at regional scales. In the Anthropocene, climate and habitat diversity alone are insufficient to explain community structure. However, until recently, ecologists lacked accessible, synthesized data describing anthropization gradients, which limited studies to macro-ecological scales. Yet, a deeper understanding of how anthropization shapes species pool and local communities is crucial for biodiversity conservation, especially in historically anthropized areas.

Location

France

Time period

2010-2020

Major taxa studied

Butterfly

Methods

Using a high-resolution (20 m) anthropization map describing anthropization on a continuous gradient across France, we examined the influence of landscape anthropization on taxonomic, functional, and phylogenetic diversities and composition of butterfly communities in Brittany (France). This taxon is known to be widely impacted by landscape changes and is an indicator of ecosystem health. We compiled 175,000 butterfly occurrences recorded from 2010 to 2020, spanning 2,447 communities across the anthropization gradient with multi-facet biodiversity indices.

Results

We showed that anthropization significantly shapes community structure, sometimes even exerting a stronger influence than habitat diversity or landscape heterogeneity. Relationships between anthropization and community diversity within the same biogeographical region were often linear rather than Gaussian, with diversity decreasing as anthropization increased. Highly anthropized sites hosted communities with lower habitat and dispersal specialization and lower species richness.

Main conclusions

These results highlight the importance of landscape matrix and typical habitats, rather than habitat quantity, in shaping biodiversity. Integrating local scale anthropization in public policies and conservation strategies is essential for effective ecological conservation and restoration.

KEY WORDS - anthropogenic pressures; beta diversity; biodiversity scale; citizen sciences; macroecology; naturalness

Introduction

Anthropization leads to major changes in global biodiversity (Ellis et al., 2013; Lyons et al., 2016; IPBES, 2019). Declines in taxonomic (Fang et al., 2023), functional (Sol et al., 2020), and phylogenetic diversities (Ribeiro-Neto et al., 2023) have been observed across several taxa in anthropized ecosystems (Montràs-Janer et al., 2024). Anthropization drastically alters landscape and habitat, for instance, through deforestation and habitat fragmentation (Bergerot et al., 2010b; Cantera et al., 2022). Human activities can also have more indirect pressures, such as pollution (whether chemical or not), which reshape species distribution and community composition (Sanders and Gaston, 2018; Zhang et al., 2022). Human activities also promote spread of non-native species, introducing new interactions between invasive and native species that may further threaten biodiversity (Doherty et al., 2016).

The impacts of anthropization on ecosystems, including habitat fragmentation, pollution, and urban heat islands, are well-documented (Haddad et al., 2015; Ogidi and Akpan, 2022; Tommasi et al., 2022). However, understanding anthropization full effect on biodiversity requires analyzing these human pressures together as few studies have done so far (Su et al., 2021; Danet et al., 2024). In addition, human impacts must be broken down to a fine scale (Vallet et al., 2010). By using gradients and different spatial scales to measure anthropization, studies highlight the response of biodiversity to human activities (Cantera et al., 2022; Callaghan et al., 2024), even in historically anthropized territories (Rivest and Kharouba, 2024). Considering anthropization, particularly in landscape, requires a gradient of human impacts in space.

To assess the anthropization impact on biodiversity, cumulative human disturbances maps have been developed. One such too is the *global map of the human footprint* (Sanderson et al., 2002), which provides an universal reference for studying anthropization. This map has been used to measure the impact of anthropization from species at the landscape scale (Arrondo et al., 2020) to taxa and ecosystems globally (Williams et al., 2020; Plumptre et al., 2021). Other methods were developed to use maps of anthropization but always at world scale (Su et al., 2021) or large scale (Callaghan et al., 2024). Macro-ecological studies on anthropization effect now leverage new data sources like citizen sciences repositories (Callaghan et al., 2024), though challenges such as incompleteness remain (Troia and McManamay, 2016). These spatial scales also have to account for the fluence of other factors such as climate (Montràs-Janer et al., 2024). In addition, species within the same region may respond differently to landscape anthropization, with some thriving while others decline (Filgueiras et al., 2021). To better understand biodiversity changes, anthropization must be compared with other factors known to impact ecological communities, such as environmental factors (Wearn et al., 2019). Therefore, a more detailed description of landscape anthropization at local or regional scales (i.e. few hundred kilometers; Hortal et al., 2010) is essential.

Anthropization does not always lead to consistent patterns of changes. The most commonly described pattern followed a bell-shaped curve where biodiversity peaks at an intermediate level of disturbance, reflecting the greatest level of ecological niche heterogeneity. This pattern was found in several taxonomic groups such as birds (Battisti and Fanelli, 2016; Guetté et al., 2017), spiders (Tajthi et al., 2017), millipedes (Bogyó et al., 2015), or algae (England et al., 2008). This aligns with the intermediate disturbance hypothesis (Connell, 1978), or the diversity-disturbance hypothesis (Huston, 1979). For these hypotheses, only a few species can survive high levels of disturbance. Biodiversity is therefore low. On the contrary, at low levels of disturbance, competition becomes the process controlling communities, also reducing biodiversity. Biodiversity would therefore be highest at intermediate levels of disturbance, as species resistant to both extremes of the disturbance gradient are found here. However, the idea of a perturbation optimum was criticized both theoretically and empirically (Fox, 2013). Recent studies have shown linear patterns, where biodiversity increases in well-preserved landscapes (Pereira and Navarro, 2015). This have been found in arthropods (Gallou et al., 2017; Dufek et al., 2024) and birds (Concepción et al., 2015). Determining which of these two models dominates, particularly in anthropized areas, is crucial for shaping effective biodiversity policies. These conflicting results highlight the need for further investigation.

This study focuses on butterflies, which are good ecological indicators of ecosystems and biodiversity state (Bergerot et al., 2011; Luppi et al., 2018; Pignataro et al., 2023). Butterflies are landscape-dependent and, except few migratory species, have limited dispersal capacity (Stevens et al., 2013). They are sensitive to environmental alteration and landscape modification (Olivier et al., 2016; Lourenço et al., 2020; Szabó et al., 2022). Through plant-butterfly interactions, some species are habitat specialists, while others are generalists and found in a large range of different habitats. Butterflies are declining in several countries, especially due to habitat loss and degradation (Warren et al., 2021; Habel et al., 2022). Many species, including a large part of the *Lycaenideae* family, rely on plants that only thrive in natural or semi-natural areas. Agriculture intensification reduces the presence of host plants, limiting species survival (Börschig et al., 2013; Szabó et al., 2022). As anthropization progresses, butterfly communities tend to become increasingly dominated by generalist species at the expense of specialist species (Clark et al., 2007; Börschig et al., 2013).

Disentangling the role of various factors (anthropic, ecological, climatic…) in shaping communities, should be a key objective (Coutant et al., 2023). We address three questions: (i) Can butterfly communities (richness, specialization) across taxonomic, functional, and phylogenetic facets be shaped by the anthropogenic gradient, especially in historically anthropized regions? (ii) If the gradient influences community structure, are community richness and specialization greater at intermediate levels of anthropization, or do they increase linearly along the gradient? (iii) How does anthropization drive community structure in comparison to environmental factors? We hypothesize that: (1) anthropization influences species presence/absence through a filtering effect (Filgueiras et al., 2021); (2) generalist species dominate at intermediate disturbance level; and (3) traits related to habitat and dispersal are favored at high levels of anthropization (Hendrickx et al., 2009; Bergerot et al., 2010a).

Material and methods

Study area and butterfly data collection

We analyzed butterfly communities in Brittany, a peninsula in France bordered by the Atlantic and influenced by a maritime climate. Brittany is historically highly anthropized, predominantly bocage landscape dominated by agriculture land use (over 64%), yet it contains diverse environments, including coastal areas, heatland, peatlands, and various wooded areas. The butterfly dataset was compiled from the regional atlas (Buord et al., 2017), and citizen-science records (https://www.faune-bretagne.org), including only recent records from 2010-2020 to align with available land use maps (see below). Finally, this dataset contains 175,416 occurrences (Fig. 1b), across 84 butterfly species for 2010-2020 (87% of the data). Analyses were conducted using presence-absence data only, as abundance data lacked standardization due to varying sampling methods.

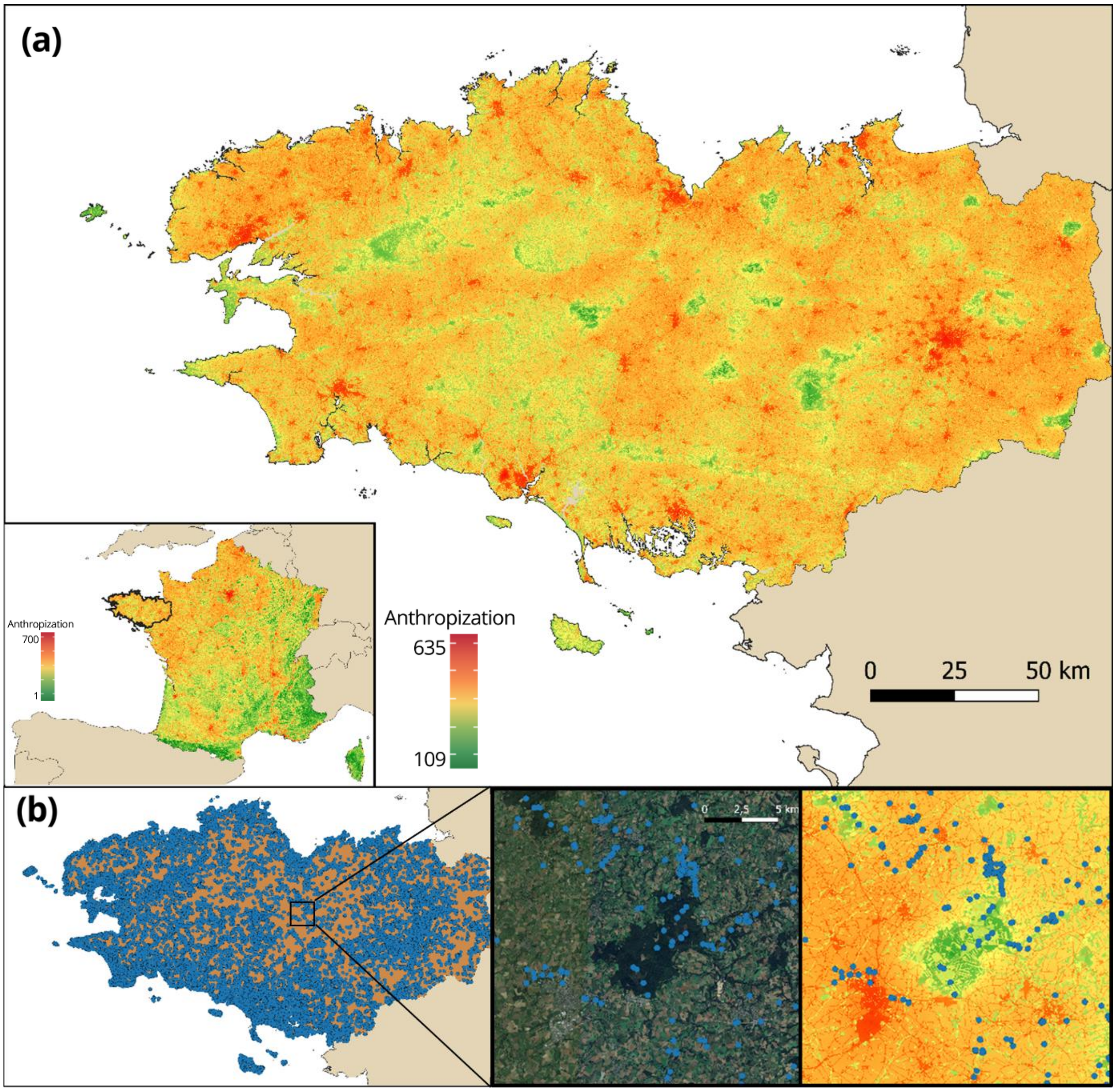

Figure 1: a) Study area. The anthropization values are between 1 and 700 for France. In Brittany, the lowest value of anthropization is 109 and the maximum is 635. b) Repartition of the 175,416 butterfly observations (blue points) in the 2010-2020 decade. Comparison of Brittany territory with anthropization map. Anthropization values can have a large range inside a same grid cell.

Completeness and community data

To create the community dataset, we first aggregated species occurrences across five geographic scales (1 km², 4 km², 16 km², 36 km², and 64 km²), retaining only one occurrence per species per grid cell to minimize detection bias.

To ensure the compiled communities accurately represent field conditions, we assessed the sample completeness using the *KnowBR* package (Lobo et al., 2018). We included communities with > 50 % completeness, i.e., comparison between predicted and observed species richness in data; an occurrence/species ratio > 3; and a slope < 0.3. These thresholds are proposed by authors as intermediate thresholds and are a trade-off between completeness and the number of communities. This process resulted in 15% well-surveyed communities (2,447 out of 15,851 potentials), yielding 467 communities for 1 km², 556 for 4 km², 551 for 16 km², 484 for 36 km², and 389 for 64 km² (Fig. 2).

Anthropogenic pressures: anthropization map

To assess landscape anthropization, we use the anthropization map from the CARTNAT Project (Guetté et al., 2021) which evaluated anthropization across France on a continuous scale from 1 to 700 for France (https://uicn.fr/cartnat-premier-diagnostic-national-des-aires-a-fort-degre-de-naturalite/). This gradient summarizes three dimensions of anthropogenic pressures as defined by Guetté et al. (2018): (1) biophysical integrity, using six layers to assess hemeroby; (2) spontaneity, using road distance and building density as proxies of human influence of natural processes; and (3) spatial continuity assessed with using omnidirectional connectivity methods via the Omniscape model. The map has a 20-meter resolution (Fig. 1a). In our study, community anthropization correlated above 70% with these three anthropogenic dimensions for each spatial scale.

To compare each grid cell, we calculated the mean anthropization values, as this metric provided the widest value range across the different spatial scales.

Landscape heterogeneity and habitat diversity

We also test the influence of landscape structure and habitat diversity using the “Carte des Grands Types de Végétation” (CGTV) from the Brittany Botanic Conservatory (CBNB; Sellin et al., 2021), which classifies the habitats into classes. The map was rasterized to a 20-meter resolution to match the anthropization map. Landscape heterogeneity was assessed by calculating marginal entropy (see formula in Nowosad and Stepinski, (2019)) with the *lsm_l_ent*() function of the “landscapemetrics” (Hesselbarth et al., 2019).

Habitat diversity, was measured with the Shannon index for each grid cell with the *diversity*() function in the “vegan” package (Oksanen et al., 2024).

Biogeographical area

To allow comparison across landscapes with similar species pools and control for community dissimilarity due to species distribution, we clustered sampling grids into biogeographical areas based on species composition, following the framework of Dapporto et al. (2015) in the “recluster” R package. We compiled all species occurrences in 100 km² squares which is the scale used by Buord et al. (2017) for the regional Atlas. Species composition for each grid cell was assessed with the Jaccard index, and a dendrogram was created to identify clusters (Fig. S1) with clustering method “ward.D2” and a random reorganization of the original dissimilarity matrix (Dapporto et al., 2015). Four biogeographical areas were then defined and refined with expert judgment: “Plain” (148 grid cells, 41% of Brittany), “Relief” (94 grid cells, 26% of Brittany), “Coastal” (75 grid cells, 21% of Brittany), and “Southern” (40 grid cells, 11% of Brittany).

Alpha diversity & specialization index

To describe communities along the anthropization gradient, we used several indices covering the three facets of biodiversity (taxonomic, functional phylogenetic). We characterized the diversity and the specialization of communities. The indices are listed below; detailed calculation methods are provided in the Appendix.

We characterized community richness with 3 indices: species richness, functional richness by using FRic index, and phylogenetic richness by using Daniel Faith’s PD metric.

To assess community specialization, we used a habitat specialization index (Julliard et al., 2006), and three Communities Weighted Means (CWMs) on hostplant family, hostplant specificity, and hostplant index (see Middleton-Welling et al., (2020) for formula). For dispersal specialization, we applied CWMs on minimal and maximal voltinism, flight duration, wing morphometric and intraspecific variation (Middleton-Welling et al., 2020). Only results for maximal voltinism, flight duration, and hostplant specificity are presented in the results, for other traits, see Appendix (Fig. S4).

We calculated the Nearest taxon index (NTI), based on the mean nearest neighbor phylogenetic distance (MNTD) to assess phylogenetic diversity.

We calculated these indices using the ”vegan” package (Oksanen et al., 2024), the “mFD” package (Magneville et al., 2022), and the “picante” package (Kembel et al., 2010).

Beta diversity index

Beta taxonomic diversity was measured using the “betapart” R package (Baselga and Orme, 2012)., with the *beta.pair()* function to calculate the beta dissimilarity and distinguish between turnover and nestedness (Baselga, 2010). The Jaccard dissimilarity index was used, and ten categories were created based on anthropization intervals between quantiles (0–1, in steps of 0.1). We focused on comparisons between the lowest anthropization category (“q90_q100”) and others. Dissimilarity values were explained by the anthropization difference between communities (Bishop et al., 2015).

For the beta functional diversity, we applied the same method as the taxonomic part. We used the *functional.beta.pair()* function of the “betapart” package considering all traits but limiting the analysis to two dimensions to reduce computation time. Beta phylogenetic diversity was calculated similarly to the taxonomic diversity using the *phylo.beta.pair()* function in the “betapart” package (Baselga and Orme, 2012).

Statistical analysis

To assess the role of anthropization and environmental variables on community assemblages, we ran linear models for each taxonomic, functional, and phylogenetic variable across all scales. For the full dataset (all biogeographical areas), depending on the distribution of response variables, we used general linear mixed models (LMM) or generalized linear mixed models (GLMM) with Gamma/Beta distribution (“lme4” package (Bates et al., 2015). Anthropization, landscape heterogeneity, and habitat diversity were included in the models. We performed backward selection keeping anthropization in all models and selecting the model with the lowest Akaike Information Criterion (AIC). We also tested anthropization as a quadratic term and chose the model with the lowest AIC between linear and quadratic forms. This allowed us to understand how response variables responded to disturbances, i.e. according to which pattern (Ostermann, 1998; Pereira and Navarro, 2015). Landscape heterogeneity and habitat diversity were combined when collinearity between them was below 0.7. The same was applied to anthropization and these variables. Biogeographical area was used as a random factor in all the models.

To characterize the role of spatial structure of communities and to deal with spatial autocorrelation detected by Moran's I test, we added, for each model, an autocovariance variable based on neighborhood distance and weight. We chose a neighborhood distance of 10 km based on semi-variograms.

The R^2 or Pseudo R^2, depending on the distribution family, was calculated. The effects of both fixed and random variables were examined. For significant variables (p-value < 5%), variances were reported. The same method was applied for each different biogeographical area with the random factor removed.

For the alpha scale, we decomposed the variance explained by anthropization, ecological variables (landscape heterogeneity and habitat diversity), spatial structure, and biogeographical area. The decompositions revealed wed mean variances for each spatial scale across the three facets.

For the beta diversity indices, we applied the same method excluding the spatial structure variable and biogeographical variables. Anthropization, landscape heterogeneity, and habitat diversity were expressed as the difference in value between the two communities being compared.

Analyses were performed using Rstudio (R version 4.2.1).

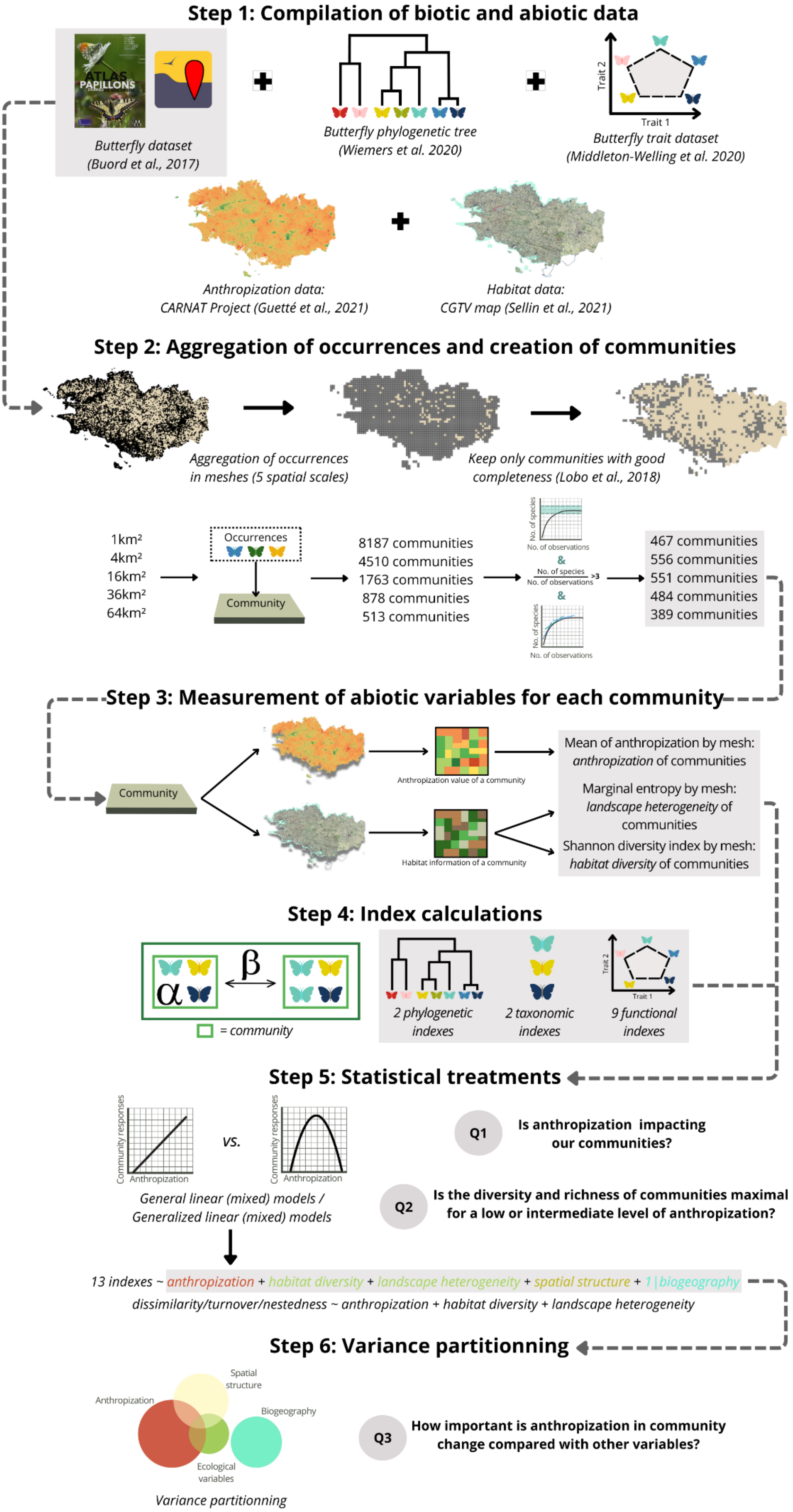

Figure 2: Step-by-step analytical framework, including (1) Data recovery, (2) aggregation at community level and (5) statistical processing. The various stages are detailed in the "Material and methods" section.

Results

The total number of species across the spatial scales ranged from 77 species (1 km²) to 83 species (64 km²). Species richness of our communities ranged between 2 species and 57 species. In Brittany, over 60% of species were present across the full gradient, while 40% were restricted to specific part of the gradient, modifying the community composition (Fig. S2).

No overall correlations were found between anthropization importance and spatial scales. The patterns depended on the response variable studied or no pattern was found. Here, we only present results for 1 km², the more realistic spatial scale. Results for other spatial scales are provided in Appendix (Fig. S4).

Alpha diversity index

In Brittany (all biogeographical areas compiled) and for all biogeographical areas except Southern region, we found a significant effect of anthropization on the species richness in 1 km² communities ($p\text{-value} < 0.05$). In Brittany and Coastal area, peaked at intermediate anthropization (Fig. 3). The variances in community richness, explained by anthropization in these areas, were respectively 12% and 22%. In the Plain and Relief areas, species richness decreases linearly along the anthropization gradient with explained variances of 22% and 8%, respectively. No effect of anthropization was found in the Southern area.

For 1 km² (and other spatial scales), correlations between species, functional, and phylogenetic richness were above 89% (Fig. S3). Due to their high correlation with species richness, we chose not to build models for functional and phylogenetic. We concluded that the trends in these indices along the anthropization gradient were similar to those of species richness.

For NTI, we found a quadratic relationship in Brittany (Fig. 3), with a minimum at intermediate anthropization values (variance = 3%). At extreme anthropization values, NTI was higher, indicating phylogenetic clustering of species within communities. In the Coastal area, NTI decreased linearly along the anthropization gradient, suggesting a decrease of clustering of species (variance = 3%). In the Plain, Relief, and Southern areas, NTI increased linearly, indicating high phylogenetic clustering at higher anthropization levels. The variance for these areas was 8%, 2%, and 9%, respectively.

Alpha specialization index

Habitat specialization of communities decreased significantly (p-value<0.05) along the anthropization gradient in Brittany, Plain, and Relief (Fig. 3), explaining 7%, 21%, and 14% of the variance, respectively. In the Coastal area, a quadratic relationship was observed, with maximum specialization at intermediate anthropization levels, accounting for 6% of variance. No significant effects were found for Southern area.

For maximal voltinism (number of generations per year), quadratic relationships were found for Brittany and Coastal area with minimum of voltinism at intermediate anthropization levels (Fig. 3). The variances were 16% and 12%, respectively. Linear relationships were found for Plain and Relief with a variance of 32% and 24%, respectively. No significant effect of anthropization was found for Southern area.

For flight duration, a quadratic relationship was found in Brittany (Fig. 3), with the minimum at intermediate anthropization levels, explaining 15% of the variance. In the coastal area, flight duration decreased linearly along the anthropization gradient (variance = 5%). Conversely, Plain, Relief, and Southern areas exhibited linear increases, explaining 21%, 15%, and 16% of the variance, respectively.

Hostplant specificity showed significant linear increases (from monophagous to polyphagous) along the anthropization gradient in Brittany, Coastal, and Plain areas (variance = 6%, 19%, and 9%, respectively). No significant effect of anthropization was found for Relief and Southern areas (Fig. 3).

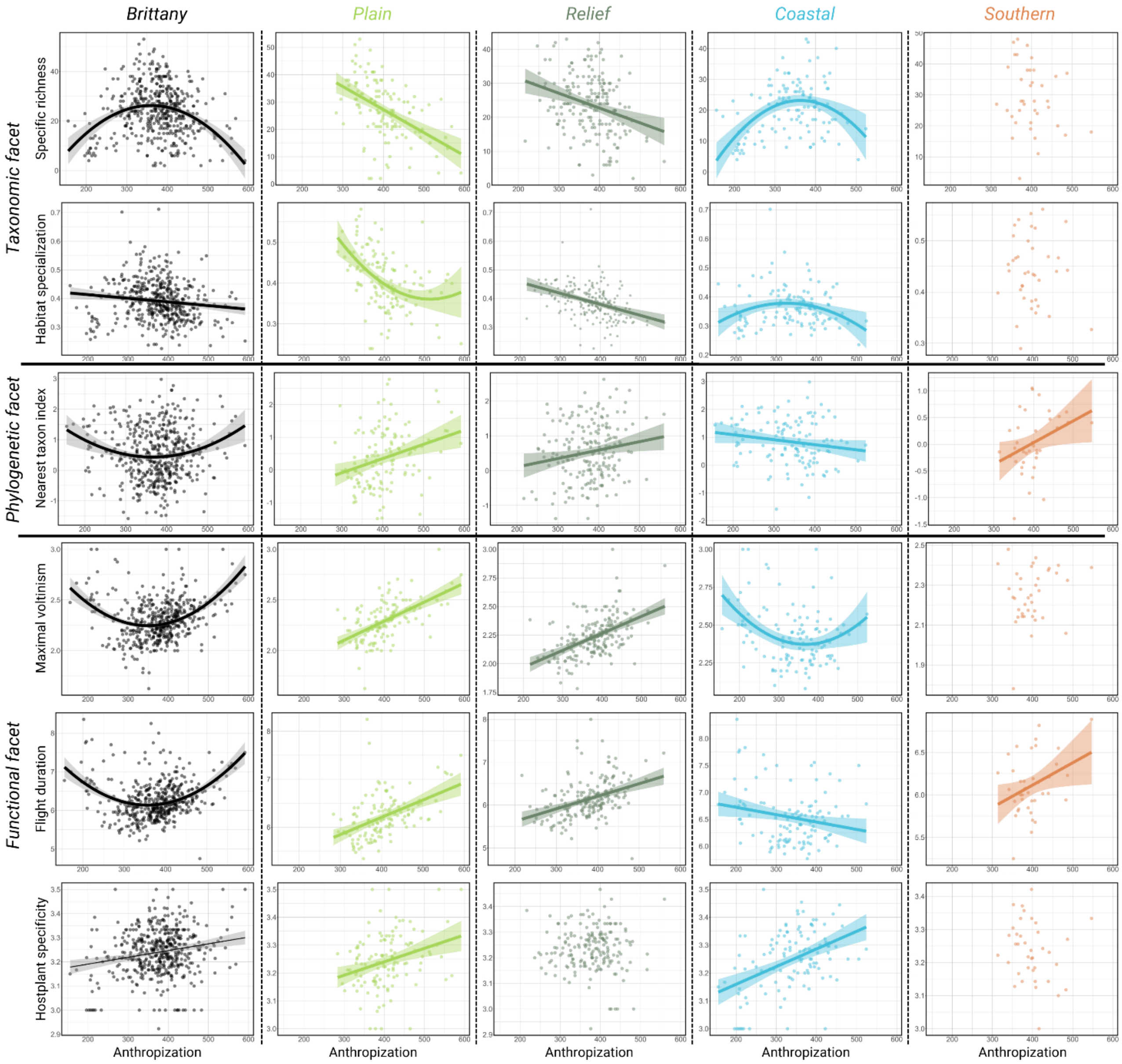

Figure 3: Variation of butterfly communities along anthropization gradient by using different indices representative of the three facets (taxonomic, functional, phylogenetic). Results for Brittany as a whole and decomposed for each of the four biogeographical areas. Only the scale of 1km² is represented. See Appendix (Fig. S4) for other scales.

Variance partitioning and abiotic variables

Anthropization explained about 10% of variance in taxonomic indices across scales (Fig. 4), except at 64 km², where it explained only 3% of the variance. The redundancy with other variables was low except at 16 km² (8%). Ecological variables were key factors in describing communities at the three largest scales (13%-34%). For these three scales, the redundancy was high with spatial structure and biogeography of communities (8%-18%). Spatial variable related to spatial autocorrelation explained significant portions of variance at the three largest spatial scales (>21%). Biogeography constantly influenced communities, with redundancy increasing at the largest spatial scales (7%-17%).

Anthropization explained 7% - 9% (Fig. 4) of the variance in functional traits across all spatial scales, with few redundancies, reaching a maximum of 4% with other variables. The importance of ecological variables increasing with spatial scales (2%-19%), with high redundancy at 64 km² (11%). The effect of spatial structure was, with a maximum of 4%. Biogeography explained between 5 % and 11% of the variance.

Anthropization explained more variance of the phylogenetic facet at the smallest (1 km², 6%) and largest (64 km², 9%) spatial scales gradient (Fig. 4), with few redundancies between anthropization and other variables. The variance of ecological variables increased with spatial scale (1%-10%). The spatial variable was particularly important to explain communities at 1 km² (11%). Finally, biogeography was constant at approximately 3% except at 1 km² (8%). High redundancies were observed between biogeography, spatial structure, and ecological variables.

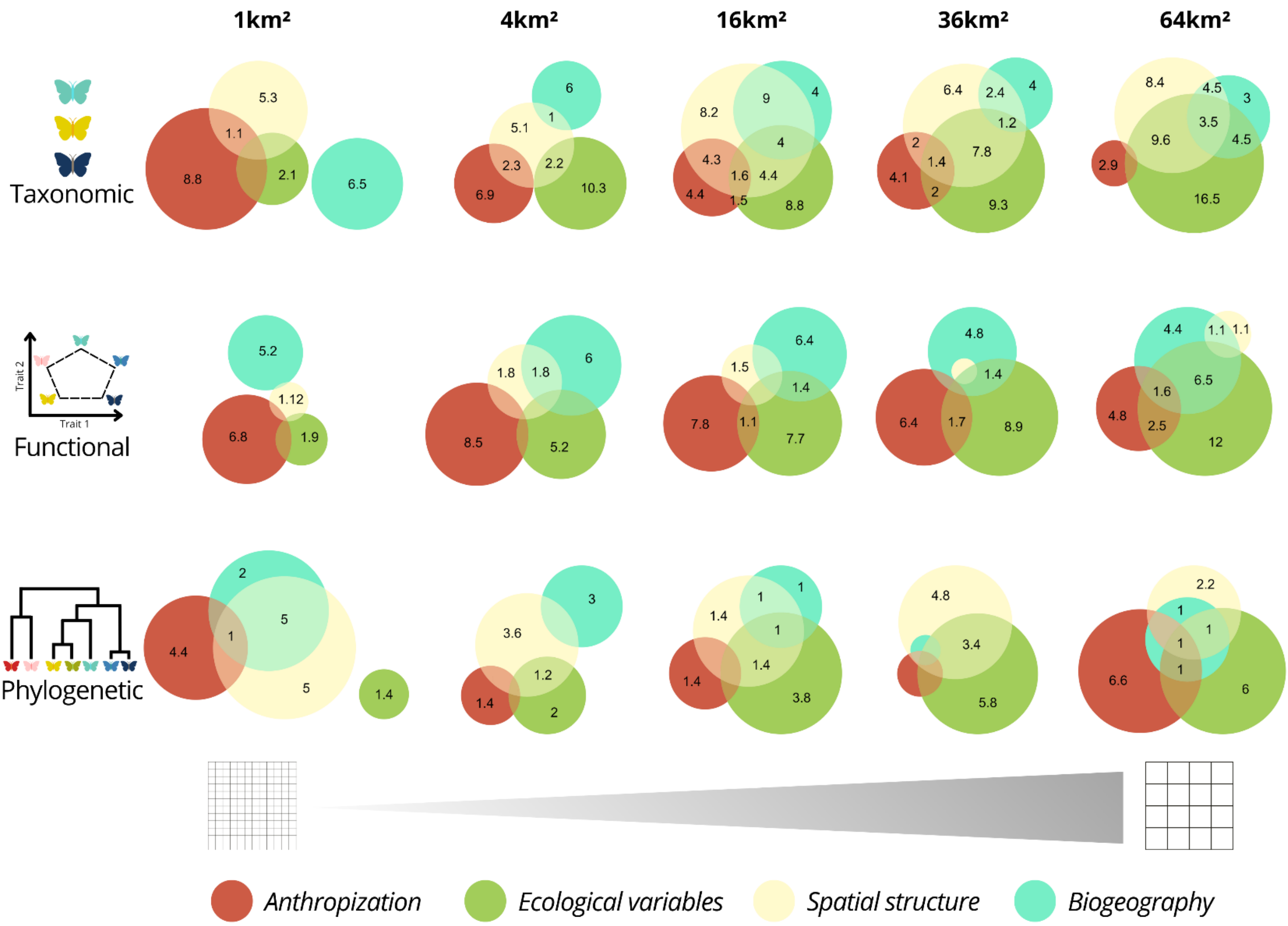

Figure 4: variance partitioning of the four types of explanatory variables (anthropization, ecological variables, spatial structure, biogeography) for alpha indices and each spatial scale. The variance partitioning is decomposed according to the facet. 10 models were done for taxonomic facet and each spatial scale. 40 models were done for functional facet and each spatial scale. 5 models were done for phylogenetic facet and each spatial scale. Biogeography was not present in the same number of models due to models realized for different biogeographical not considering this variable. It appeared in 2 (taxonomic), 8 (functional), and 1 (phylogenetic) model for each spatial scale.

Beta diversity of communities

Taxonomic, functional, and phylogenetic dissimilarities varied significantly, with the same patterns (Fig. 5), along anthropization gradient (p-value < 0.05). Taxonomic dissimilarity increased with anthropization difference with maximum values between 60% and 70% of dissimilarity. Anthropization explained between 4 and 9% of the variance, with 21% explained at 64 km². Phylogenetic dissimilarity showed similar trends, with maximum values between 45% and 55%, and anthropization explained between 5% and 23% of the variance, increasing with scale. Functional dissimilarity was lower, with maximums close to 35%-50%. Anthropization explained between 3% and 20% of the variance, also increasing with scale. For all facets, relationships between dissimilarity and anthropization differences were linear at 16 km², 36 km², and 64 km² and quadratic for 1 km² and 4 km² with maximum dissimilarity occurring at a anthropization difference of 250-300.

Turnover showed significant relationships with anthropization at all spatial scales for each facet, with a greater increase in turnover observed at both ends of the anthropization gradient (Fig. 4). For the taxonomic facet, turnover increased from 25-45% to 30-55%, with anthropization explaining less than 3% of the variance. For the functional facet, turnover increased from 0-10% to 15-20% but variances explained by anthropization were lower than 1% except at 64 km² (7%). For the phylogenetic facet, turnover increased from 15-25% to 20-30% and variances were lower than 2% across all spatial scales.

Nestedness showed significant relationships across all spatial scales (Fig. 4), with contrasting patterns according to the spatial scales. Linear increases in nestedness were found at 16 km², 36 km², and 64 km², while quadratic trends were found at 1 km² and 4 km², with a maximum for intermediate anthropization differences. For the taxonomic facet, nestedness increased from 5-15% to 20-25% at the three largest spatial scales with maximums of 25-30% for spatial scales with quadratic trends. Variance explained by anthropization ranged from 1% to 7%. For the functional facet, nestedness increased from 0-10% to 25-30% for 16 km², 36 km² and 64 km². The maximums of 1 km² and 4 km² were reached for 25-40% of nestedness. Variances explained ranged from 2% to 14% with higher values at larger spatial scales. For the phylogenetic facet, nestedness ranged from 5-10% to 25-30% at 16 km², 36 km² and 64 km². The maximums of 1 km² and 4 km² were reached with 20-30% of nestedness. Variances explained by anthropization (2-13%) increased with spatial scales.

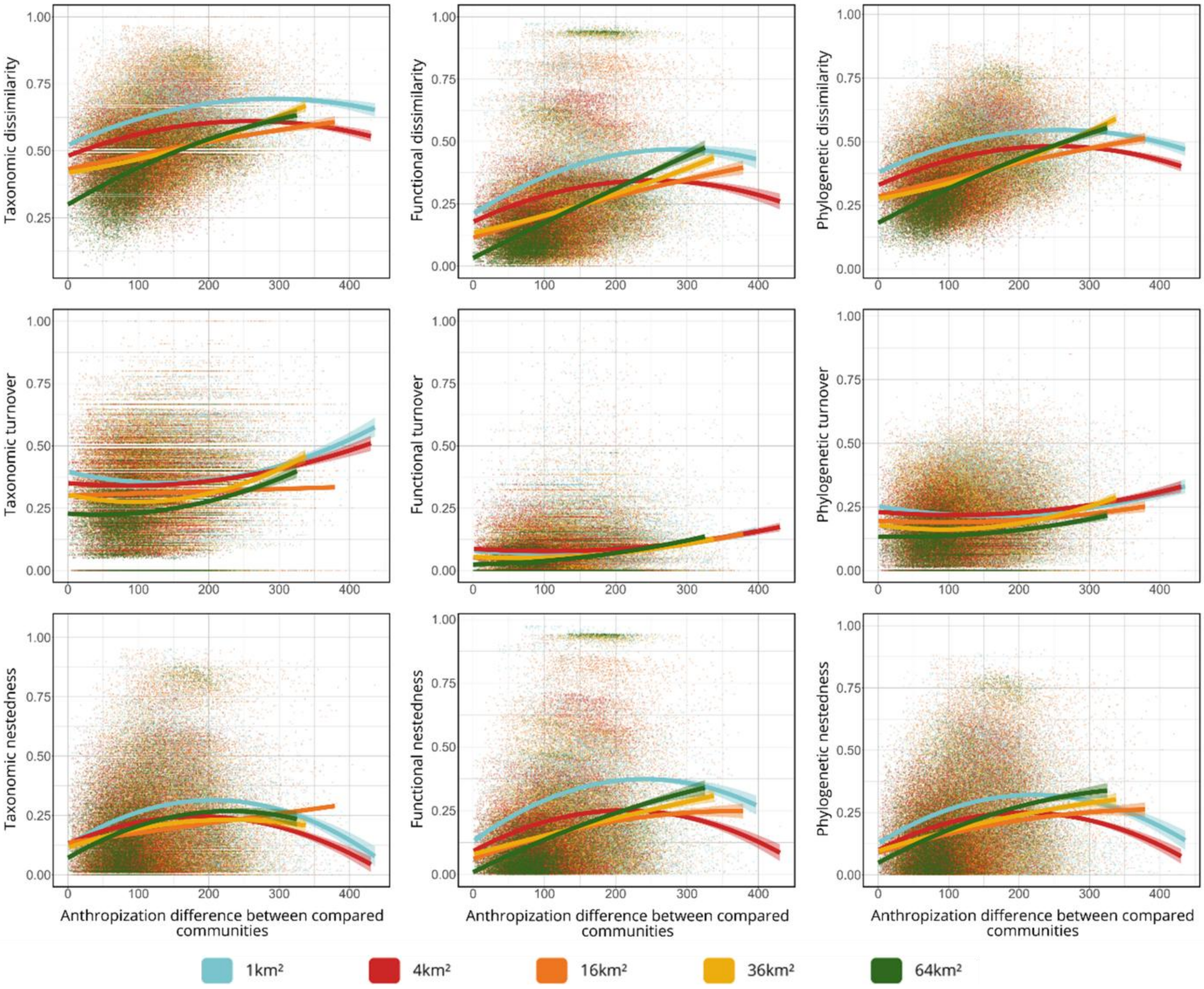

Figure 5: beta diversity of butterfly communities by using the Jaccard dissimilarity, Jaccard turnover, and Jaccard nestedness indexes. Results decomposed for the three facets. Colors represent different spatial scales.

Discussion

We highlighted how butterfly communities are structured in a highly anthropized French region. We found that anthropization played a key role in community structure and composition. Above all, we found that relationships between anthropization and different biodiversity descriptors were not systematically Gaussian, contrary to what was often reported in the litterature (Callaghan et al., 2024). When studying these relationships within biogeographic areas accounting for species distribution differences, we shown that anthropization induces a linear decrease in several descriptors such as species richness, specialization, or phylogenetic diversity. Furthermore, anthropization was complementary, rather than redundant, to habitat diversity (López-González et al., 2015) and landscape heterogeneity (Estrada-Carmona et al., 2022), to explain community assembly. At the landscape scale, these habitat diversity and landscape heterogeneity are classically recognized as important factors shaping biodiversity, especially arthropods (Hendrickx et al., 2007; Sattler et al., 2010).

Linear decrease in richness along the anthropization gradient

At the regional scale, the intermediate disturbance hypothesis (Connell, 1978) seemed to be verified, as the maximal species richness, along with functional richness and phylogenetic richness (all correlated), were reached at intermediate anthropization levels. When comparing communities with similar climates and biogeography, linear patterns are dominant at all the spatial scales, with a decrease in richness with higher anthropization levels. This relation was consistent across numerous indices describing the communities and supporting the idea that the increase in anthropization systematically reduces biodiversity. This relation aligns with several studies that consider anthropization as a multi-factorial disturbance (e.g., Gallou et al., 2017; Dufek et al., 2024).

Quality of habitat over quantity

The decrease in species richness, and more generally of biodiversity, according to anthropization can be explained by different filters. There is a limited availability of ecological niches in more anthropized landscapes (Warren et al., 2001; Zeni et al., 2019). Butterflies have limited interspecific competition and are thus particularly influenced by hostplant availability (Nakadai et al., 2018). Our results showed that habitat diversity did not explain much of the variance in communities (Fig. S5). Instead, the typicity of habitats in preserved landscapes promote species richness (Summerville and Crist, 2004; Tobisch et al., 2023). Communities in these areas tend to have a higher degree of habitat specialization. Many species preferentially found in communities with the lowest anthropization level, such as *Plebejus idas, Euchloe crameri,* or *Spialia sertorius*, which depend on unique habitat like limestone grasslands and moorlands (Buord et al., 2017). Conversely, *Cacyreus marshalli* was identified as a strong synanthrope, i.e., living preferentially in anthropized environments (Fontaine et al., 2016; Tzortzakaki et al., 2019).

If these species are found only in these environments, it is probably due to the strong affinity between their host plants and these habitats. Hostplant specificity (monophagous vs. polyphagous) supports this idea, because the communities in a well-preserved landscape are more similar to monophagous than polyphagous ones. The ability of butterflies to locate a habitats with their host plants is key to their presence (Tudor et al., 2004). Some species are evolutionarily linked to well-defined host plants (Kunte, 2007; Tiple et al., 2009; Bergerot et al., 2010a). For example, *Pseudophilotes baton,* a species extremely sensitive to anthropization (Konvicka et al., 2008), is primarily found in dry moorlands and scrublands, specializing in rare plant species at a regional scale such as *Thymus vulgaris*, *Thymus serpyllum* or *Thymus praecox* (Konvicka et al., 2008; Buord et al., 2017; Moussus et al., 2022). These plants require very extensive grazing to thrive. Higher levels of anthropization could, through direct disturbance (e.g., mowing, pesticide) or indirect disturbance (e.g., temperature with urban heat island), prevent certain host plants from thriving due, for example, to their inability to complete their entire growth cycle (Holden et al., 2007). Anthropization can also modify plant phenology, leading to potential mismatch between hostplant and butterflies (Li et al., 2019; Fisogni et al., 2020).

Nestedness and homogenization patterns in anthropogenic landscapes

Another result is the shift in community composition along the gradient. The presence of habitats in low-anthropization landscapes and the specialization of species for these environments drives this change, found in taxonomic, functional, and phylogenetic dissimilarity. When analyzing shift in community composition along anthropization gradient, we found high nestedness for intermediate levels of anthropization. This indicates species loss between communities in landscapes with low and intermediate levels of anthropization. The increase in anthropization corresponds to the loss of types of habitats (wetlands, wet moorlands, dry moorlands…) and therefore to their related specialist butterfly species. Other studies already demonstrated a nested pattern along fragmentation gradients (Hendrickx et al., 2009; Hill et al., 2011).

The disappearance of specialist species along anthropization gradients supports the idea of biotic homogenization (McKinney and Lockwood, 1999), which was observed both in functional traits (Concepción et al., 2015) and phylogenetic diversity (Morelli et al., 2016). These results corroborate the idea that biodiversity should not only be measured by species richness but also by the identity and characteristic of the species present (Filippi-Codaccioni et al., 2010; Concepción et al., 2015). However, Cisneros *et al.* (2015) criticize the interpretation of nestedness in the case of fragmentation, arguing that species richness should not be the only focus and that landscape variables must be integrated. They found that communities at both ends of the landscape anthropogenic gradient were mainly driven by species turnover.

Species turnover at both ends of the anthropization gradient

Some species can benefit from anthropization if it favors conditions that align with their ecological niche. Species turnover, i.e., the change in species along a gradient, occurs especially when comparing communities with the highest and the lowest anthropization levels. This recruitment of new species corresponds to anthropogenic communities that gain synanthropic species or generalist species do not present in well preserved landscape due to low competitive ability. Some studies have focused on the role of non-native species in this turnover, because they are mainly present in anthropized environments, facilitating the emergence of their ecological niche (La Sorte et al., 2008; Fuentes-Lillo et al., 2021). However, as far as we know, only *Cacyreus marshalli* is a non-native species that has benefited from urbanization (Quacchia et al., 2008), and abundance of its host plants (*Pelargonium spp.*) in Brittany. New species could follow this trend and colonize Brittany soon (Ruffener et al., 2024). Other studies showed the key role of turnover with species only present in communities with high levels of anthropization (Fornal-Pieniak et al., 2019; Rolls et al., 2023). Another explanation of this turnover could also result in the use of substitute habitat in more anthropized landscape due to the degradation or disappearance of their original habitats (Martínez-Abraín and Jiménez, 2016).

Although our study demonstrated linear decreases in biodiversity along the anthropization gradient, even at a regional scale, some points still need further exploration to deepen our understanding of the role played by the landscape. If we worked on reaggregated communities in space and time, it would be interesting to validate our results by studying “real” ecological communities *sensus* Tansley (1935), i.e. those involving real ecological interactions between species.

Understanding how biodiversity is influenced by anthropization is a major issue to act efficiently in conservation and ecological restoration projects. This work demonstrates that anthropization maps, which aggregate cumulative impacts, can be a relevant and useful tool for characterizing communities at a regional scale. The importance of the landscape in communities structure seems to be a key factor. The use of anthropization maps at this scale could help identify landscapes at risk to provide insights for conservation and restoration efforts. Moreover, taking anthropization into account could open up new avenues for predicting biodiversity response to landscape ecological restoration projects.

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Data Accessibility Statement

Community dataset and R scripts for index calculation and analysis are available on Figshare:

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Supporting information for "Landscape anthropization drives composition and diversity of butterfly communities at a regional scale" Bongibault *et al.*, 2025

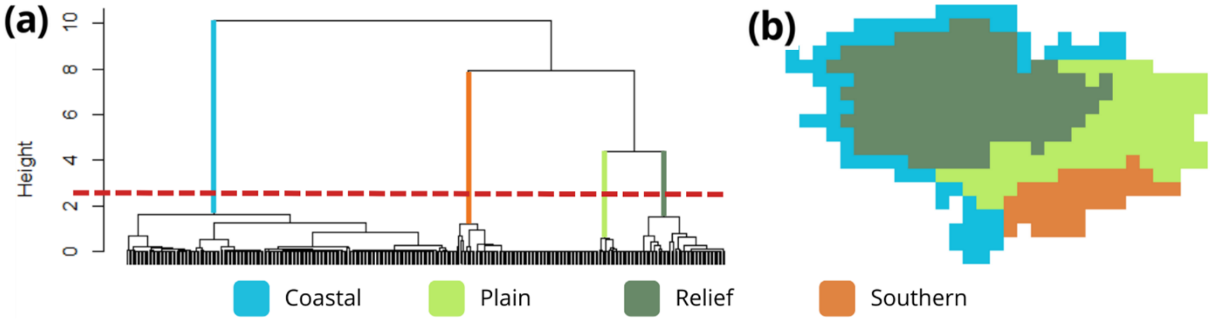

Figure S1: a) Dendrogram of grouping 100km² communities according to their species composition, with Jaccard index. Red line corresponds to level where the number of biogeographical areas was kept. b) Representation of the 100km² cells with their value of biogeographical area after standardization of categories by expert opinion.

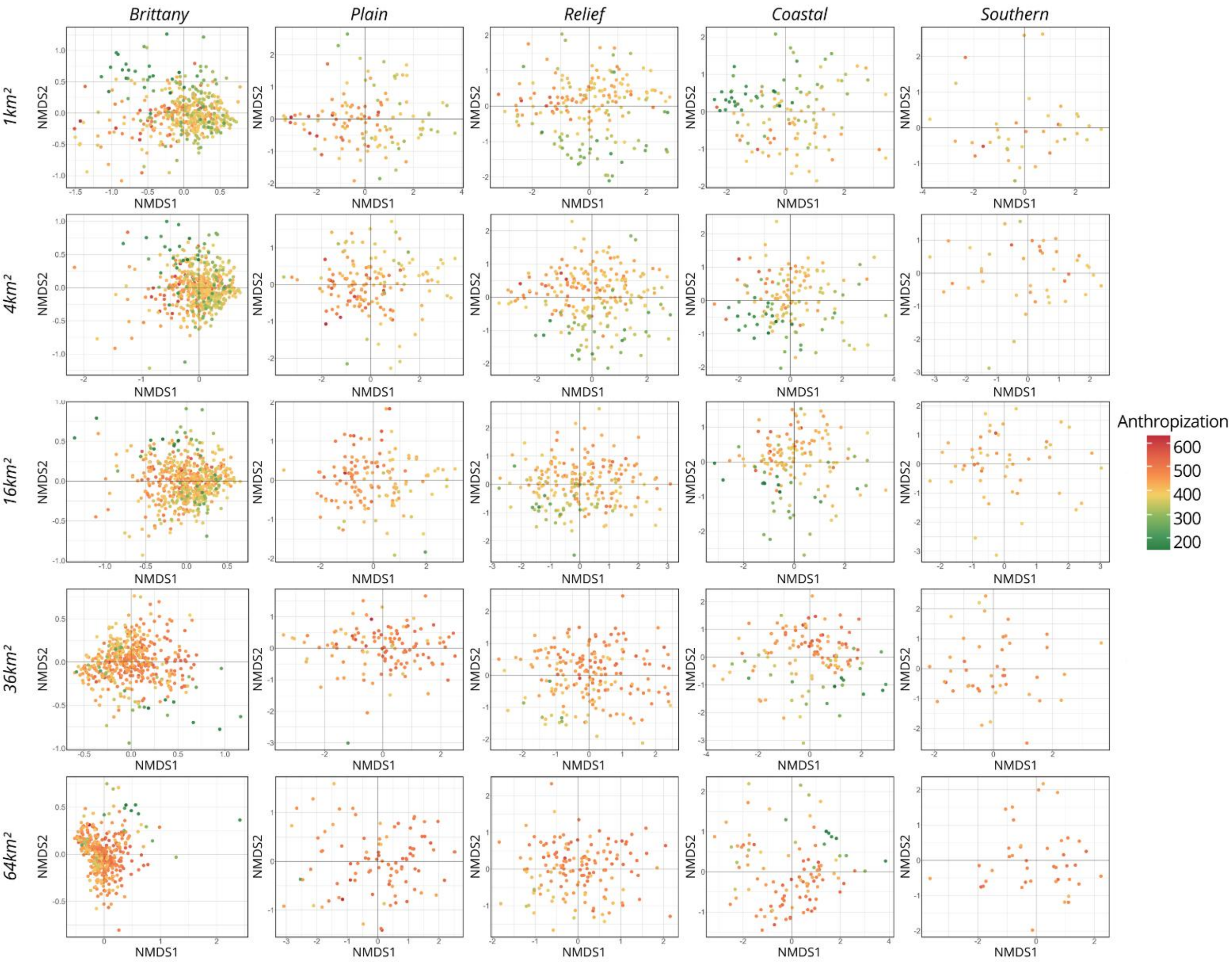

Figure S2: Non-metric Multidimensional Scaling (NMDS) for each of the five spatial scales. Results are presented for Brittany and decomposed for the different biogeographical areas.

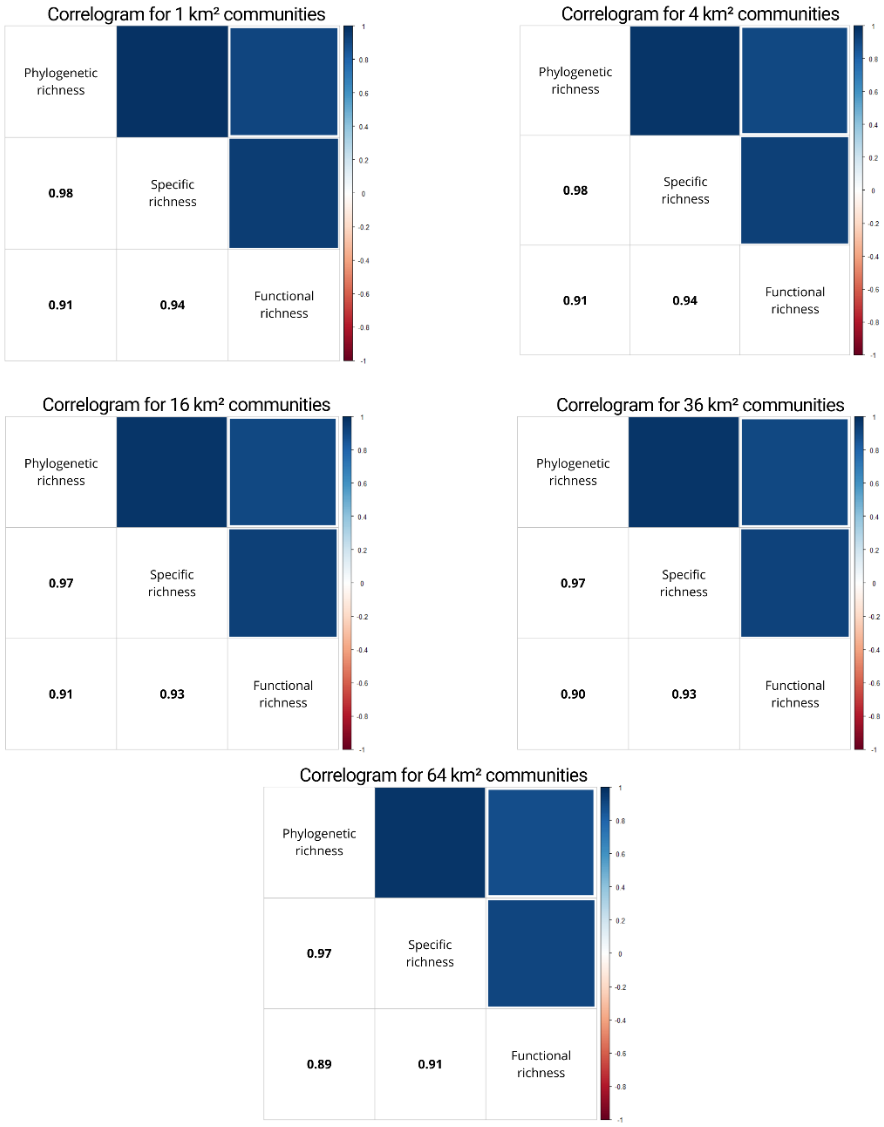

Figure S3: Correlation of richness indexes (taxonomic, functional, phylogenetic) for the five spatial scales.

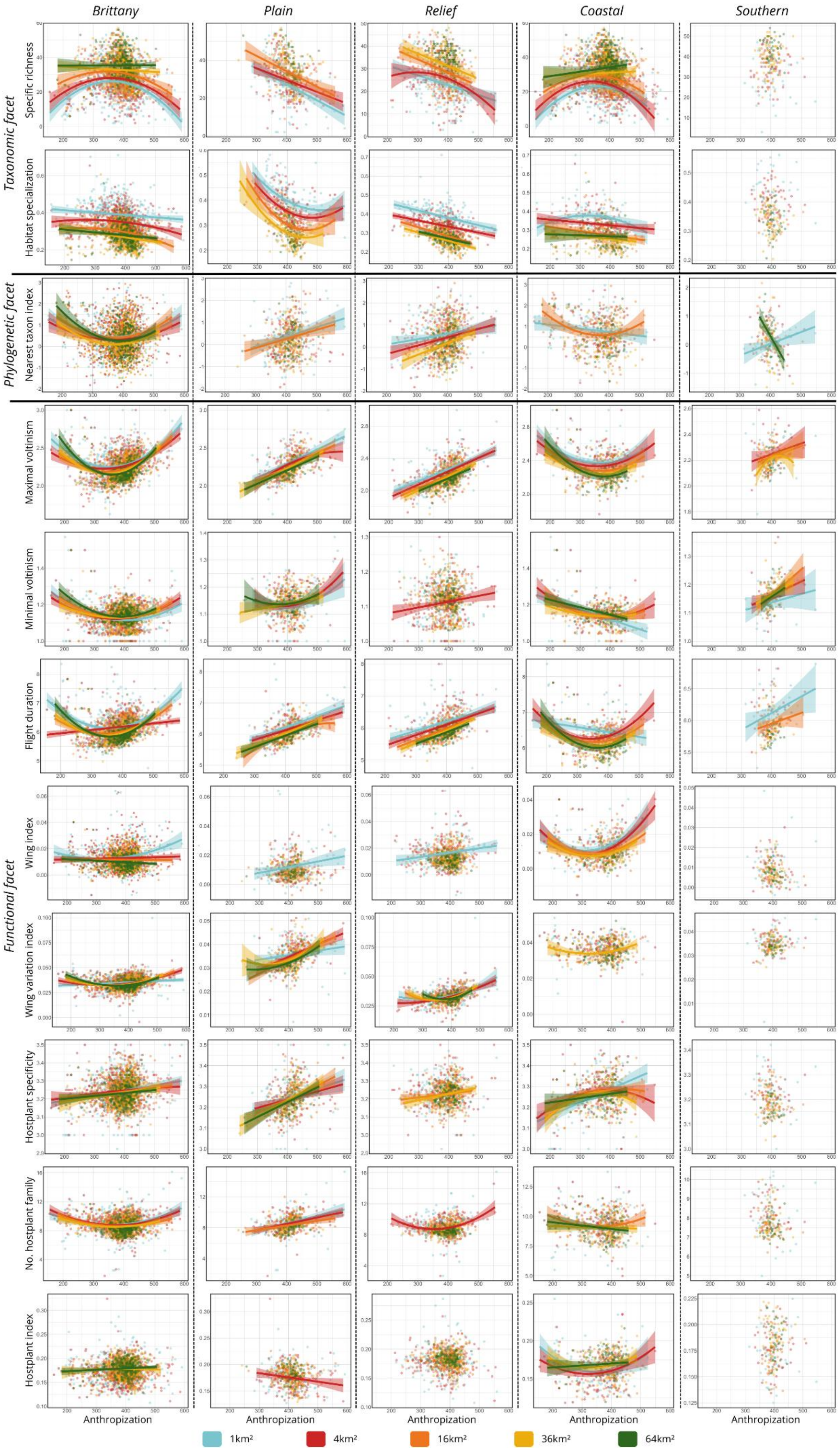

Figure S4: Relationship between taxonomic, phylogenetic, and functional indexes and anthropization. Results are presented for Brittany and the four biogeographical areas. Patterns are represented only for significant relationships (p-value<0.05). Colors correspond to different spatial scales.

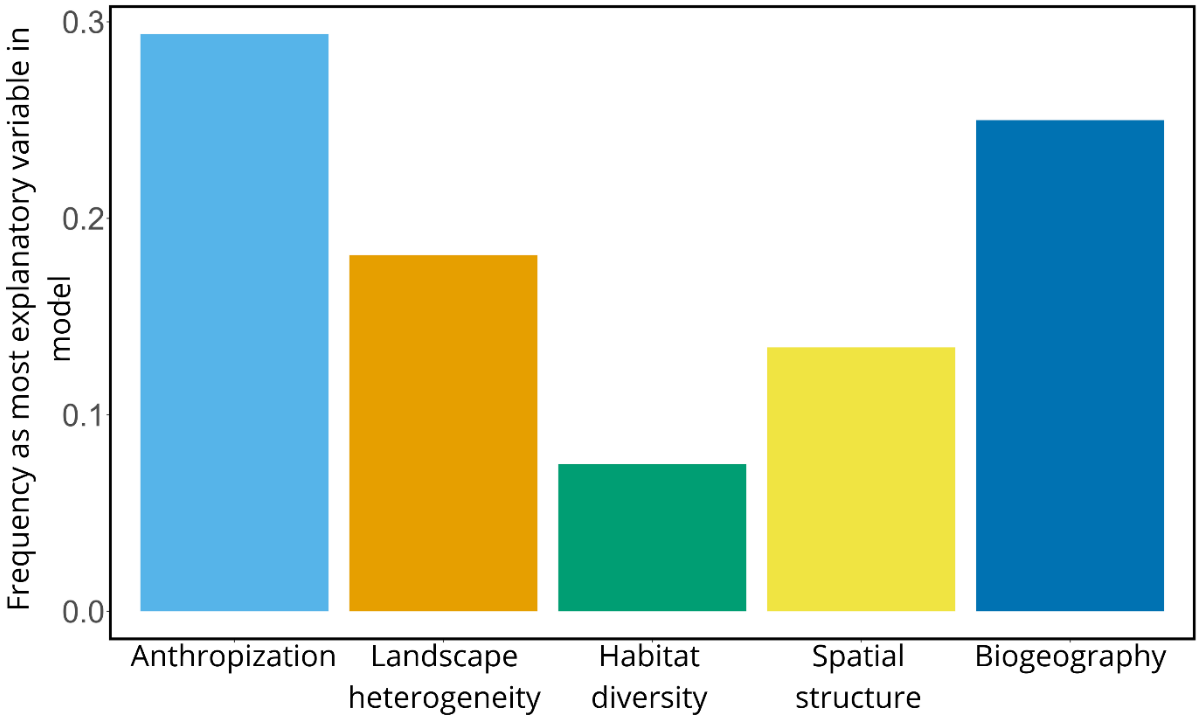

Figure S5: Frequency, for each explanatory variable, as the most explanatory variable in the model. The frequency is based on 320 models for all variables except biogeography which were only present in models for Brittany (64 models). Models where two variables had the same variance explained and represented the highest variance have not been considered.

Material and methods

Taxonomic alpha diversity index

Two indexes were calculated to characterize the alpha taxonomic part (richness and specialization) of communities. We measured species richness (number of species) with the *specnumber()* function of the "vegan" package (Oksanen et al., 2010).

We calculated an index of species habitat specialization (SSI) by using the method of Julliard et al. (2006). The formula is: $SSI = \left(\frac{\mathrm{H}}{\mathrm{h}} - 1\right)^{\frac{1}{2}}$ where H is the total number of available habitats and h the number of habitats used by the species. We used the CGTV habitat value of each occurrence in the community dataset to measure the number of habitats and the specialization index for each species. The mean of the index was calculated for each community by considering the score of species only once even if the species was seen several times in the grid cell.

Functional alpha diversity index

To assess functional diversity, we used the trait database of Middleton-Welling and al. (2020), which compilated 25 traits for 542 species in Europe and Maghreb. We, therefore, selected 8 traits that consider (i) the dispersion capacity (maximal and minimal voltinism, wing morphometric and its intraspecific variation, flight duration) and (ii) feeding habitat preference information (hostplant family, hostplant specificity, hostplant index (see Middleton-Welling et al., 2020 for formula)). These traits correspond to proxies of dispersal and feeding specialization with, for example, a lower number of generations, a shorter time of flight duration, a smaller wing for dispersal specialists, and a lower number of hostplant families of higher hostplant specificity for feeding specialists. Only maximal voltinism, flight duration, and hostplant specificity are described in the result. Other functional traits are presented in Supplementary materials.

We also calculated the functional richness (FRic) with the “mFD” package (Magneville et al., 2022). After analyzing the quality of the representation, we decided to measure functional richness based on the first five axes. We had to eliminate communities with fewer than 6 species. Only the 1 km^2 and 4 km^2 scales had communities involved (maximum 10 communities). As these communities were homogeneously represented along the naturalness and environmental gradients, there was no influence on the results. In addition, we characterized communities with Community Weighted Mean (CWM) for each trait with the *functcomp()* function of the “mFD” package (Laliberté et al., 2014).

Phylogenetic alpha diversity index

To assess phylogenetic diversity we used the phylogenetic tree developed by Wiemers et al. (2020) for European species. The phylogenetic richness was measured by considering Daniel Faith's PD metric which sums the branch lengths of all co-occurring species from the same community (Faith, 1992). To complete the alpha phylogenetic description, we calculated a diversity index with the Nearest taxon index (NTI). This variable is based on the mean nearest neighbor phylogenetic distance (MNTD) and uses the standardized effect size mean phylogenetic (pairwise) distances. NTI allowed us to have access to the general structure pattern occurring in communities and was sensitive to the clustering and overdispersion close to the tips of a tree. Thanks to this index, we have information about phylogenetic clustering or over-dispersion of the species inside communities compared with the expected random assembly. These metrics were computed with the "picante" package (Kembel et al., 2010).

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