

RESEARCH ARTICLE

Journal of
Biogeography

WILEY

Associating the structure of Lepidoptera-plant interaction networks across clades and life stages to environmental gradients

Hsi-Cheng Ho^{1,2} | Florian Altermatt^{1,3}

¹Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

²Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

³Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, Switzerland

Correspondence

Hsi-Cheng Ho and Florian Altermatt, Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland. Email: hsichengho@gmail.com and florian.altermatt@ieu.uzh.ch

Funding information

Swiss National Science Foundation, Grant/Award Number: 310030_197410; University of Zurich Research Priority Program in Global Change and Biodiversity (URPP GCB); Yushan Young Fellow Program (MOE, Taiwan)

Abstract

Aim: The spatial-structural patterns of plant-insect interaction networks, particularly their associations with landscape-scale environmental factors, remain poorly understood. We apply data-driven network constructions that integrate biogeographic and trophic interaction knowledge to uncover how Lepidoptera-plant networks vary across environmental gradients in a real-world landscape.

Location: The 36,000 km² German state Baden-Württemberg, Central Europe.

Taxon: Lepidoptera insects and angiosperm plants.

Materials and Methods: We integrated extensive data of Lepidoptera-plant occurrences and interactions to infer local interaction networks across Baden-Württemberg, encompassing 3148 plant and 980 Lepidoptera species, covering butterflies, Noctuid moths, Geometrid moths, and Bombycoid moths. We quantified clade- and life-stage-specific network structures and related them to GIS-informed environmental conditions, thereby revealing the spatial (environmental) patterns and potential drivers of network variations.

Results: Spanning shared environmental gradients, Lepidoptera clades and life stages formed various interaction structures with plants and exhibit distinct spatial-structural patterns. For all Lepidoptera groups, except Geometrid moths, potential diet across life stages broadened toward low-elevation farmlands. The larval and adult networks of butterflies became less modular with farmland coverage; the same for adult Noctuid moths, but the inverse for adult Geometrid moths. With increasing elevation, the larval and adult networks of Noctuid moths became less and more modular, respectively, whereas Geometrid adult networks became more modular. While the adult dietary niche of butterflies overlapped more at low elevation, those of Noctuid and Geometrid moths further associated with land cover and overlapped more toward low- and high-elevation farmlands, respectively.

Main Conclusions: The spatial-structural patterns of Lepidoptera-plant networks vary along geo-climate and land-cover gradients in ways depending on the Lepidoptera's clade and life stage. The driving mechanisms likely include both evolutionary (e.g., resource-consumer [co-]evolution) and ecological (e.g., competitive exclusion) processes, and differentially affect Lepidoptera across clades and life stages. These findings pinpoint conservation implications at both species and community levels, with

potential trade-offs for managing different Lepidoptera-plant communities under environmental changes.

KEYWORDS

butterfly, geo-climate influence, insect-plant interaction, land-cover influence, life stage, moth, network structure, spatial pattern

1 | INTRODUCTION

Species occurring in the same habitat can interact inextricably with each other, forming interaction networks whose features affect the persistence, stability, and functioning of the whole community (Bascompte, 2009; Thompson et al., 2012). While certain environmental factors, such as geo-climate and land-cover drivers, have been shown to strongly influence species occurrence and hence biodiversity (e.g., Mantyka-Pringle et al., 2015), the understanding on how interaction networks vary across environmental gradients is far more recent and comparatively limited (pioneers, e.g., Tylianakis et al., 2007; Woodward & Hildrew, 2002). Yet, for a needed, better biodiversity management in the Anthropocene, it is essential to understand these interaction structures and their dependencies on key factors across realistic landscapes (Lau et al., 2022; Pellissier et al., 2018; Thompson et al., 2012; Tylianakis et al., 2010; Tylianakis & Morris, 2017). Indeed, recently, we see emerging case studies working toward such a direction (Frelat et al., 2022; Ho et al., 2022; Kortsch et al., 2019; Liu et al., 2021; Neff et al., 2021), suggesting a responsiveness of interaction networks to environmental gradients.

Plant-insect interaction networks are often of particular interest because they cover many species playing important roles in ecosystems. Among all, the Lepidoptera-plant system is arguably best-studied, since Lepidoptera are hyper-diverse and form a prevailing component in terrestrial ecosystems worldwide (Scoble, 1995). The holometabolous lepidopterans play 'dual roles' interacting with plants. In most cases, their larvae are herbivorous, whereas adults utilise floral resources and serve as pollinators (Boggs, 1987). This encompasses both antagonistic and mutualistic relationships and, interestingly, often across the same Lepidoptera-plant species pairs (Altermatt & Pearse, 2011). Thus, disentangling the potentially divergent network patterns between Lepidoptera life stages interacting with the same local plant assemblages could reveal both the positive and negative interaction structures and their implications on ecological functions (Astegiano et al., 2017). Moreover, lepidopterans depend two-fold (at both life stages) on their food plants and some have evolved into mutual dependencies (Pearse & Altermatt, 2013a; Weiblen et al., 2006), which implies a high potential for cascading effects. Hence, the system should be prone to—and thus appropriate for studying—environmental influences cascading across the whole interaction network (Kehoe et al., 2021; Pearse & Altermatt, 2013b).

Past studies on plant-insect networks suggest a typical modular structure, reflecting that sets of insects tend to interact with respective sets of plants but rarely outside such modules that they formed (Astegiano et al., 2017; Braga et al., 2018; Olesen et al., 2007), and this pattern is echoed in individual Lepidoptera-plant studies (Braga et al., 2018; López-Carretero et al., 2014; Muto-Fujita et al., 2017). However, these studies are either conducted locally with a single community or rely on spatially implicit interaction knowledge, thus missing the spatial dimensions to detect potential environmental reliance of network structure. Meanwhile, there are investigations of the geographical distributions of Lepidoptera and their food plants as global or continental integrations (e.g., Carvajal Acosta & Mooney, 2021). Yet, these studies tend to focus on a few species' co-occurrences and thus do not inform network composition and structure (but see Narango et al., 2020). Moreover, it is often the environmental gradients at a landscape scale that shape species distributions therein (Hanspach et al., 2014; Jones, 2011). While landscape-scale case studies have shown that insect- or Lepidoptera-plant network structures can change across elevation or succession gradients (e.g., Losapio et al., 2015; Neff et al., 2021; Pellissier et al., 2012), the biological coverage (regarding taxa and life stages) of these studies was limited and yet allow the formation of a general understanding. To manage biodiversity, particularly in the context of attributing environmental drivers to structuring biological interactions within communities, an improved comprehension of interaction network structures along environmental gradients is crucial yet unachieved.

Here, to fill the gaps, we build upon existing knowledge with substantial biological coverage to ask how Lepidoptera-plant network structure is influenced by key geo-climate and land-cover environmental factors at a landscape scale. Firstly, we hypothesise that environmental conditions that are unfavourable to biodiversity are also unfavourable to diverse interactions among species, and thus should generally lead to smaller and loosely connected interaction networks. Secondly, as different taxonomic groups (e.g., clades) and life stages of Lepidoptera differ intrinsically in their ways of interacting with plants, we hypothesise that environmental drivers can shape Lepidoptera-plant interaction networks through life-stage- or clade-specific traits or processes (e.g., diel activities, competition of various extents), thereby leading to inconsistent spatial-structural patterns among clades and/or between life stages. To test our hypotheses, we integrate biogeographic ('who occurs where') and interaction ('who interacts with whom and how') knowledge to disclose the structure

of antagonistic and mutualistic interactions formed by the same local assemblages of Lepidoptera and plants, as well as the structural differences among Lepidoptera clades. We therefore target the geographic variation of network structure, drawing the associations between environmental drivers and interaction networks in three aspects: (1) between Lepidoptera life stages, (2) among Lepidoptera clades, and (3) along selected geo-climate and land-cover gradients.

We based our analysis on extensive, long-term, and highly complete empirical datasets on the occurrences and interactions of Lepidoptera and plants in Baden-Württemberg, Germany (Central Europe). We applied the metaweb approach to integrate grid-based occurrence and interaction information to construct local Lepidoptera-plant networks of each Lepidoptera clade and each life stage across the study area. Environmental information of the same grid cells was derived from geographic information systems (GIS). We quantified the structure of local networks with a selected set of frequently studied network metrics and identified different structural features across Lepidoptera clades and life stages. Finally, we related the detected structures to geo-climate and land-cover gradients to reveal the environmental reliance of the spatial-structural patterns of Lepidoptera-plant networks.

2 | MATERIALS AND METHODS

2.1 | Study area and its environment

Our study area is the German state of Baden-Württemberg in Central Europe, spanning 35,752 km² and a vertical range from 85 to 1493 m above sea level. The study area was spatially resolved to 10' longitude × 6' latitude grids (roughly 10 × 10 km²). Hereinafter, we refer to such grid cells as the 'local' scale, which presents the resolution of our species occurrence, environmental variables, and constructed interaction networks (see further below). In total, our data covered 310 cells (Figure 1).

We extracted geographic, climate, and land-cover information of the study area from available GIS databases, then spatially resolved the information to match the same grids above mentioned. The variables included: mean elevation of each cell from *Shuttle Radar Topography Mission* (SRTM, NASA/NGA), mean temperature of each cell from *CHELSA*, and local land cover from *CORINE Land Cover* (CLC, EEA), all averaged over the years of 2005–2015. These variables chosen (among some alternatives) as our preliminary test showed that they presented the most parsimonious combination that best explained the environmental variation in our study area (Section S1). For land cover, we dropped cover types that generally occupy only a minimal area per cell, thereby focusing on three major (coarse yet highly distinct) types at the scale of our cells in subsequent analyses: forests (mean coverage 37.2%, range 1.3%–88.7%), farmlands (49.6%, 5.4%–93.9%), and urban areas (10.4%, 0.2%–59.3%). Further details of land-cover sorting are in Section S1.

2.2 | Data on Lepidoptera, plants, and their interactions

Our study considers Lepidoptera (butterflies and moths) and plant species that were recorded in the study area within a time window of three decades (1985–2014). All Lepidoptera considered are native to Baden-Württemberg. The plants considered were those that can be found in the wild, including all native plants, non-native plants (including invasives), and naturalised ornamental plants and crops. All occurrence data were derived from respective long-term monitoring and natural history surveys encompassing all the local cells (Database *Arbeitsgruppe Schmetterlinge Baden-Württembergs am SMNK* <https://www.schmetterlinge-bw.de> for Lepidoptera; *Bundesamt für Naturschutz 2010 & Floraweb* for native and naturalised plants). We note that the sampling followed a haphazard regime, yet the Lepidoptera monitoring was so intensive that grids were generally well-sampled for all taxonomic groups considered. Thus, although our local scale and corresponding environmental information spatially resolve the finest to the size of cells, the recorded Lepidoptera species therein should reflect local (*sensu stricto*) assemblages shaped by localised processes, yet integrated at the sampling grid. Also notably, by compiling present-absent occurrence information across such a time window, we dropped pre-1985 records where the species may no longer exist, and took advantage of the more systematically and homogeneously sampled data within the 1985–2014 time window (Figure S1). In total, the dataset contains local occurrences of 980 Lepidoptera species and 3148 plant species (a few as aggregated species complex). We then focused on four main clades of Lepidoptera in Baden-Württemberg, namely butterflies (Papilionoidea; incl. Hesperidae, Lycaenidae, Nymphalidae, Papilionidae, and Pieridae), Noctuid moths (Noctuoidea; incl. Erebididae, Noctuidae, Nolidae, and Notodontidae), Geometrid moths (Geometridae), and Bombycoid moths *sensu lato* (Bombycoidea and Lasiocampoidea; incl. Endromidae, Lasiocampidae, Lemoniidae, Saturniidae, and Sphingidae). Each of these clades is relatively diverse in the area, making them suitable subjects for among-clade comparisons. A species' occurrence record is considered to represent the occurrence of both life stages in a given cell. Consequently, we expected some sampling bias toward butterflies due to their diel-activity patterns.

To construct the Lepidoptera-plant interaction network, we compiled the dietary information of lepidopterans mainly based on the work of Ebert (1991–2005) and further complemented with few smaller datasets. The total dataset of interaction used is the same as already used by Altermatt and Pearse (2011) and Pearse & Altermatt (2013a, 2013b). This covered both their larval usage of host plants and adult usage of floral resources. Such dietary information was grounded on empirical observations of feeding under natural, un-manipulated field situations, recorded by professional entomologists over a course longer than 50 years and with more than 2.3 million observations of individual Lepidoptera-host interactions (Ebert, 1991–2005; Pearse & Altermatt, 2015). We converted the recorded interactions into binary

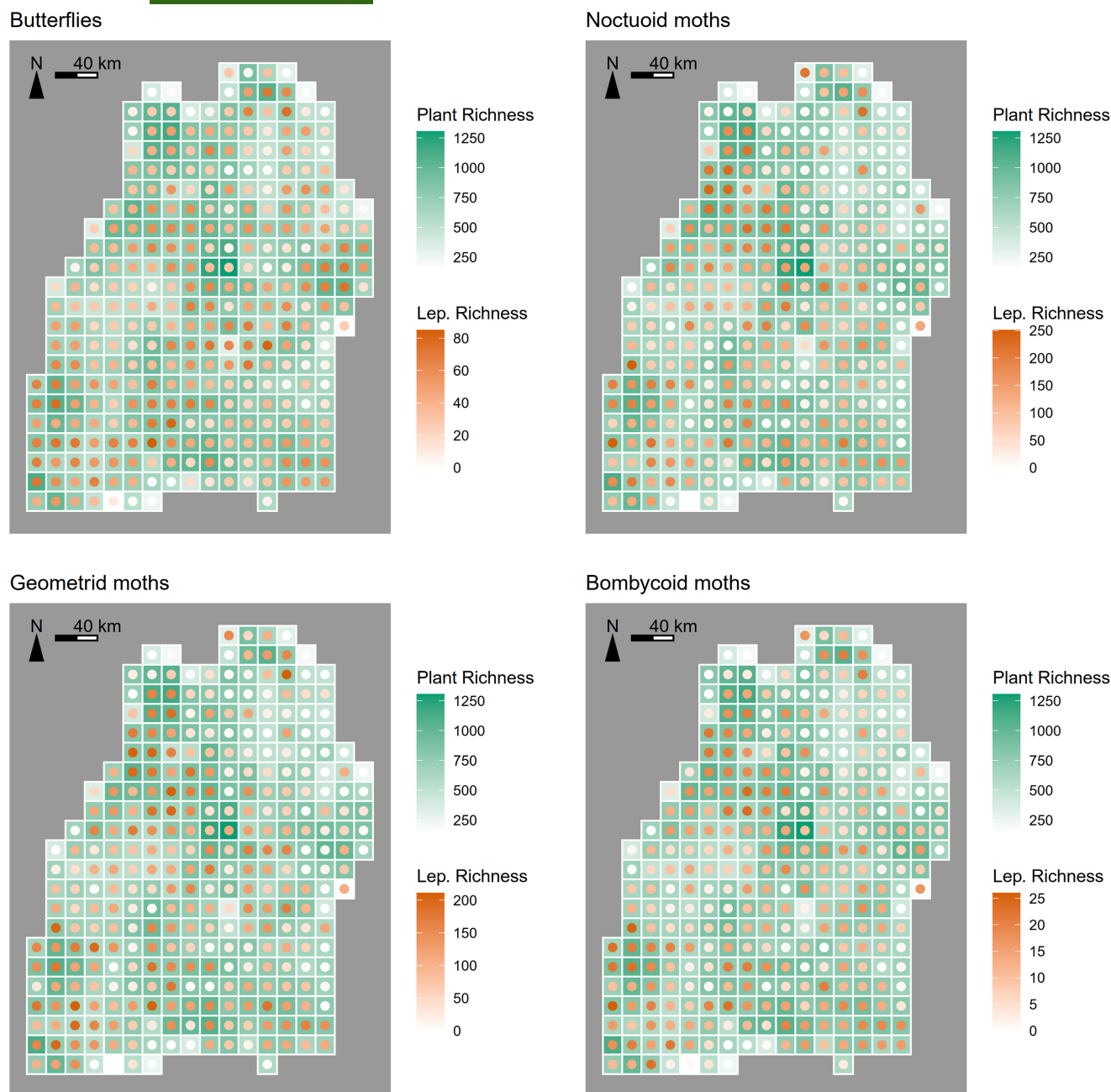


FIGURE 1 The richness of plants (local richness range: 148–1303) and Lepidoptera recorded in each of the 310 grid cells across Baden-Württemberg. The four focal clades of Lepidoptera, namely butterflies (local richness range: 0–85), Noctuid moths (0–251), Geometrid moths (0–211), and Bombycoid moths (0–26), are each presented in a subfigure. The spatial richness patterns of the three moth clades were highly consistent despite their various ranges of richness, while butterflies exhibited a somewhat different pattern. For their correlations, see Figure S2.

(interact or not) dietary matrices between Lepidoptera and plants, larval and adult stages separated. Given the enormous sampling intensity, and since we extracted only the binary information from accumulative records, we here treated our dietary matrices as being complete (Pearse & Altermatt, 2015); yet, we acknowledge that a certain degree of under-sampling may unavoidably exist in the data, particularly in nocturnal species (see also Poisot et al., 2012).

We subsequently applied the ‘metaweb’ approach (Ho et al., 2022; Saravia et al., 2022) to extrapolate local co-occurrences

of Lepidoptera and plants to local interaction networks, taking our dietary matrices as respective the larval and adult metawebs. The approach assumes that a feeding interaction indicated in the metaweb will realise if the corresponding Lepidoptera-plant species pair co-occurs locally, that is, in the cell looked at. In other words, every Lepidoptera species at a given life stage has a fixed set of potential regional food plants, which could be used locally if co-occurring. This assumption embraces the concept that interactions are driven by matching functional characteristics (e.g., chemical tolerance in

Lepidoptera, see Després et al., 2007), and collapses potential intraspecific variations of these characteristics at the species level (Ho et al., 2022); note that, however, it neglects mechanisms that prevent interactions from being locally realised even with species co-occurrence, for example link formation depending on phenology or habitat quality (Poisot et al., 2012). In our case, we assumed no spatial structure and mobility restrictions of the species within the local cells, so all species present can interact. We inferred the realisation of interactions between locally (cell-level) co-occurring Lepidoptera and plants using the metawebs, thereby constructing local Lepidoptera-plant networks for each Lepidoptera clade and life stage. Species without local interacting partners (e.g., Lepidoptera adults without functioning proboscis, or plants that are not food to any focal Lepidoptera) were excluded from the networks. In other words, although at each local site there was a fixed plant assemblage, for each focal clade and life stage only the respective food-plant subset was accounted. Our constructed local networks essentially reflect potential (not locally-sampled) interactions, but importantly within empirically-derived boundaries of realistic interactions and co-occurrences. Thus, when being viewed beyond the local scale, they can guide an unbiased exploration of spatial-structural patterns of networks resulting from the compositional difference of local communities.

2.3 | Spatial diversity and network analyses

Based on our occurrence data, we derived species diversity (richness) of plants and each focal Lepidoptera clade across all 310 local grid cells. We analysed the correlations among these cell-wise richness values to check if they exhibited correlated spatial diversity patterns (Figure S2). Such patterns were also visualised on regional

grid maps of diversities (Figure 1). Then, to disentangle environmental drivers that may have contributed to these spatial diversity patterns, we conducted a principal component analysis (PCA) with cell-wise mean elevation, mean temperature, and proportional land cover of forests, farmlands, and urban areas as the explaining variables ($N=310$). The identified PC1 and PC2 (Figure 2; from a retrospect, respectively reflected geo-climate and land-cover gradients) were used as environmental predictors for a series of general linear model (GLM) analyses on lepidopterans' and plants' richness (model assumption tests see Figure S3). A significant non-zero slope detected in the analyses would indicate the corresponding PC's significant influence. The richness \times PC interaction terms were included in the lepidopteran analyses to examine potential slope differences among Lepidoptera clades.

With our constructed local Lepidoptera-plant networks (Figure S4), we quantified their structure with a selected set of structural metrics: mean generality of lepidopteran consumers, network modularity, and mean dietary niche overlap of lepidopterans. Mean generality reflects the mean diet breadth of Lepidoptera with a given local plant assemblage. Modularity indicates the prevalence of a modular structure within a network (i.e., species from the same module interact more frequently among themselves than with species from other modules; calculations see Section S2). Lepidopterans' dietary niche overlap was evaluated by their local food-plant usage (Section S2). The higher the overlap, the stronger the lepidopterans' diet competition. Niche overlap could also be evaluated from the plants' perspective, indicating their apparent competition (in antagonistic larval networks) or pollinator competition (in mutualistic adult networks). We here focused on Lepidoptera's perspective since the values from both perspectives were mostly positively correlated (Figure S5). We also addressed network connectance and nestedness, and presented relevant contents in the SI (Figures S6–S9). All

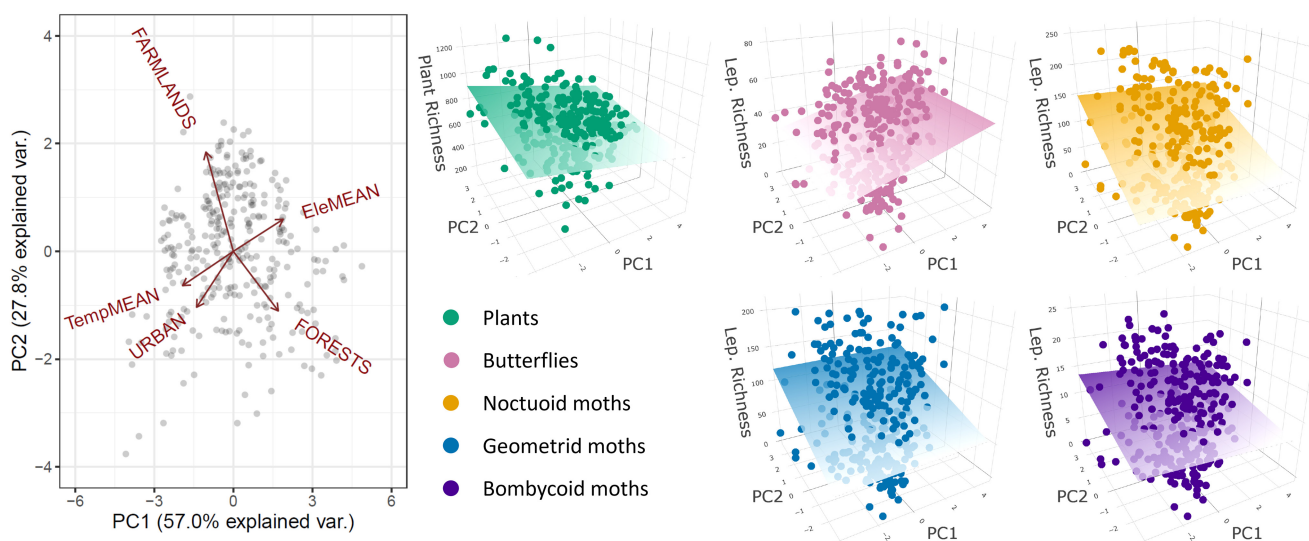


FIGURE 2 The first two principal components of environmental factors (PC1 and PC2, considered as axes of gradients), and the richness of plants and the four Lepidoptera clades across these two axes as 3D scatterplots. The planes in the 3D scatterplots are regression planes of the observed values, whose colour fade toward the low-value end. Corresponding stats with separated regressions against each PC are provided in Figures S10 and S14.

these metrics are frequently examined in ecological network studies (e.g., Ho et al., 2022; Thébault & Fontaine, 2010), as they capture not only structural features but also ecological implications spanning organismal (e.g., diet breadth) and community (e.g., niche differentiation) scales.

To resolve whether there are structural differences among the networks of Lepidoptera clades, and whether environmental drivers may have shaped their spatial-structural patterns via influencing community composition, we mirrored the analyses of species richness, performing a series of GLM of network metrics among Lepidoptera clades and each respectively against the two PCs (model assumption tests see Figure S3). Notably, for the hereinafter network analyses we excluded small local networks with either plant or Lepidoptera richness smaller than 10 (Martins et al., 2022). Small networks tend to generate unreliable and artefactual structural measurements (Dormann et al., 2009) that distort the interpretation. Thus, across all 310 cells, the number of available local networks (i.e., sample size) for each Lepidoptera clade-stage combination were: 272 and 271 for larval and adult butterflies, 251 and 239 for Noctuid moths, 252 and 236 for Geometrid moths, and 146 for larval Bombycoid moths (no remaining adult network, as most the adult Bombycoid moths considered do not have a functional proboscis).

With the detected spatial-structural patterns of local networks, to further disentangle the possible shaping mechanisms of such patterns, we applied two null models to simulate respective randomised networks. These model-generated 'counterparts' were designed to be comparable to the local networks (whose metric readings were 'observations'). The first null model is 're-assembled': with a local network at a given cell as the input, this model randomly draws Lepidoptera and plants from the study area's respective species pools, and uses our metawebs to wire them into a new local network with exactly the same number of species in both trophic levels as the input. Therefore, networks generated by this model are re-assembled Lepidoptera-plant communities where the interactions remain biologically realistic (i.e., based on realistic diets), but the real-world species-environment reliance (i.e., biogeographic 'who occurs where') is destroyed; that is, local species assemblages are randomly composed, instead of shaped by the environment via all relevant ecological or evolutionary processes determining species' spatial occurrences. The second null model is 'shuffled': with a local network at a given cell as the input, this model keeps the same number of nodes at each trophic level and the same total number of links, but rearranges the links among the nodes, thereby generating a new network. Therefore, networks generated by this model have neither biologically realistic identities nor interactions of species—both the real-world Lepidoptera-plant interdependences and species-environment reliance are destroyed. For each observed local network, we generated 20 randomised counterparts (a conservative size to avoid creating artificial significance; sensu White et al., 2014) with each null model. Looking at structural metrics' readings, if an observation lies within the confident interval estimated from its 20 're-assembled' counterparts, such observed structure is likely not shaped by real-world species-environment reliance, because

the randomly re-assembled communities already exhibit the same structure without realistic community composition. In contrast, an observation outside such a confident interval indicates a significant (positive or negative) contribution of real-world species-environment reliance on the structural feature. Similarly, an observation outside the confidence interval of 'shuffled' counterparts indicates a significant collective contribution of a real-world dependency between species (and species interactions) and the environment. We made comparisons between observed networks and null-model counterparts across the five focal network metrics to examine if the observed spatial patterns were driven by these mechanisms. We took the difference between observed value and the mean of the null-model values (former minus latter), then divided it by the standard deviation of the latter to convert the observations to Z scores. An illustration of how we unified and visualised such comparisons using Z-scores and 3D regression plots is given in Figure 3.

All quantifications, analyses, and plotting were performed using R version 4.2.1 (R Core Team, 2013). Relevant information, including applied packages and functions, is described in Section S2. The R scripts performing these tasks are accessible at the provided online repository.

3 | RESULTS

3.1 | Descriptive and species richness results

Across all 310 studied cells, the local (per cell) richness of plants averaged 730.6 ± 181.8 species (mean \pm SD), while the local richness of Lepidoptera averaged 38.1 ± 20.9 species for butterflies, 93.1 ± 69.2 for Noctuid moths, 81.9 ± 61.1 for Geometrid moths, and 10.0 ± 7.0 for Bombycoid moths (Figure 1). For each of the four focal Lepidoptera clades, local Lepidoptera richness was significantly positively correlated with local plant richness (with correlation coefficients between 0.34 and 0.4; Figure S2). Looking into further details, the three moth clades exhibited highly consistent spatial diversity patterns despite their various range of richness, whereas the butterfly clade somewhat differed from the moths (with ~ 0.9 high correlation coefficients among moth clades, while ~ 0.6 moderate coefficients between moth and butterfly clades; see Figure S2). Figure 1 shows these patterns and depicts that species diversity hotspots (dark orange dots) of moth clades were well-aligned with each other, but less aligned with butterflies.

The potential environmental contributors of observed spatial diversity differences among focal clades were revealed by our PCA of environmental factors. The first two PC axes together explained 84.8% of the environmental variation among local cells. The PC1 mostly captured the geo-climate variation, that is mean elevation and temperature, while the PC2 captured the land-cover variation, that is the coverage of forests, farmlands, or urban areas (Figure 2). Informed by the regressions against the two PC axes, the richness of butterflies was more influenced, positively, by PC1 ($R^2 = 0.04$, $p < 0.001$; Figure S10), whereas the richness of the

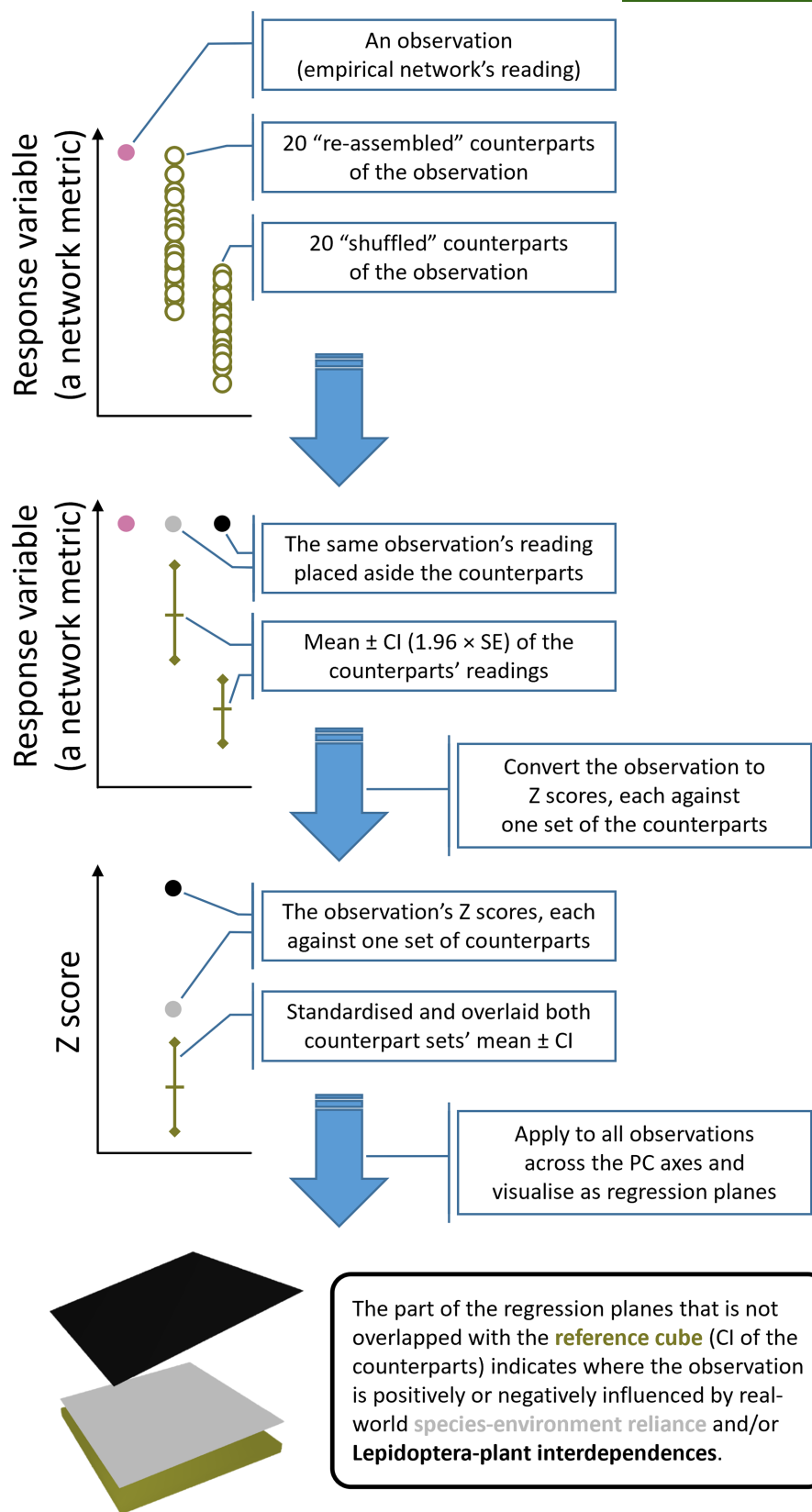


FIGURE 3 An illustration of how observations of network metrics are converted to Z scores against the two randomised counterparts (generated by 're-assembled' and 'shuffled' null models, see Section 2) to disentangle the contribution of real-world species-environment reliance and Lepidoptera-plant interdependences on shaping empirical network properties.

three moth clades were consistently more influenced, negatively, by PC2 ($R^2=0.05$, 0.04 , 0.02 and $p<0.001$, <0.001 and $=0.021$ for Noctuid, Geometrid, and Bombycid moths, respectively; Figure S10). In other words, there were more butterfly species toward high-elevation and low-temperature areas (note that the whole study area, and thus the mean elevation of every cell, was below 1500ma.s.l.), while more moth species toward farmland-dominated lands (Figure 2; Figure S10). Environmental drivers therefore did not have a consistent effect on the richness of Lepidoptera of different clades.

3.2 | Network structure across environmental gradients

With the constructed clade-specific Lepidoptera-plant local networks, we quantified and associated their structural features to the environmental PC axes, and compared the observations with null models (Figure 3). With respect to the mean generality (diet breadth) of Lepidoptera in the interaction networks, larval butterflies had the narrowest diets among the four clades, but conversely with the broadest diets as adults ($p<0.001$ for comparing with any moth

clade; Figure S11). The tendencies of mean generality varying along the PC axes were generally consistent across the four Lepidoptera clades at the larval stage. That is, higher generality toward low PC1 and high PC2, or say toward low-elevation farmlands ($R^2\geq 0.10$ and $p<0.001$ for PC1 and PC2 in butterflies, and $R^2=0.02$ and $p=0.03$ for PC1 in Geometrid moths; Figure 4; Figure S11). At the adult stage, butterflies and Noctuid moths exhibited qualitatively similar patterns as of the larvae ($R^2=0.06$ and 0.03 , $p<0.001$ and $=0.008$, respectively, for PC1 and PC2 in butterflies, and $R^2=0.03$ and $p=0.006$ for PC1 in Noctuid moths; Figure 4; Figure S11). However, an inversed pattern was detected in adult Geometrid moths, that is having broader diets toward high-elevation forests ($R^2=0.02$, and $p=0.058$ and 0.031 , respectively, for PC1 and PC2; Figure 4; Figure S11). The null-model analyses further showed that the larval generality patterns of the four clades were positively driven by real-world species-environment reliance (i.e., realistic 'who occurs where' shaped by the environment), and similarly for the adult pattern of butterflies. Instead, the adult patterns of Noctuid and Geometrid moths were negatively driven by such reliance (Figure 4).

Regarding network modularity, butterflies formed the most modular networks among the four clades as larvae, but the least modular ones as adults ($p<0.001$ for comparing with any moth

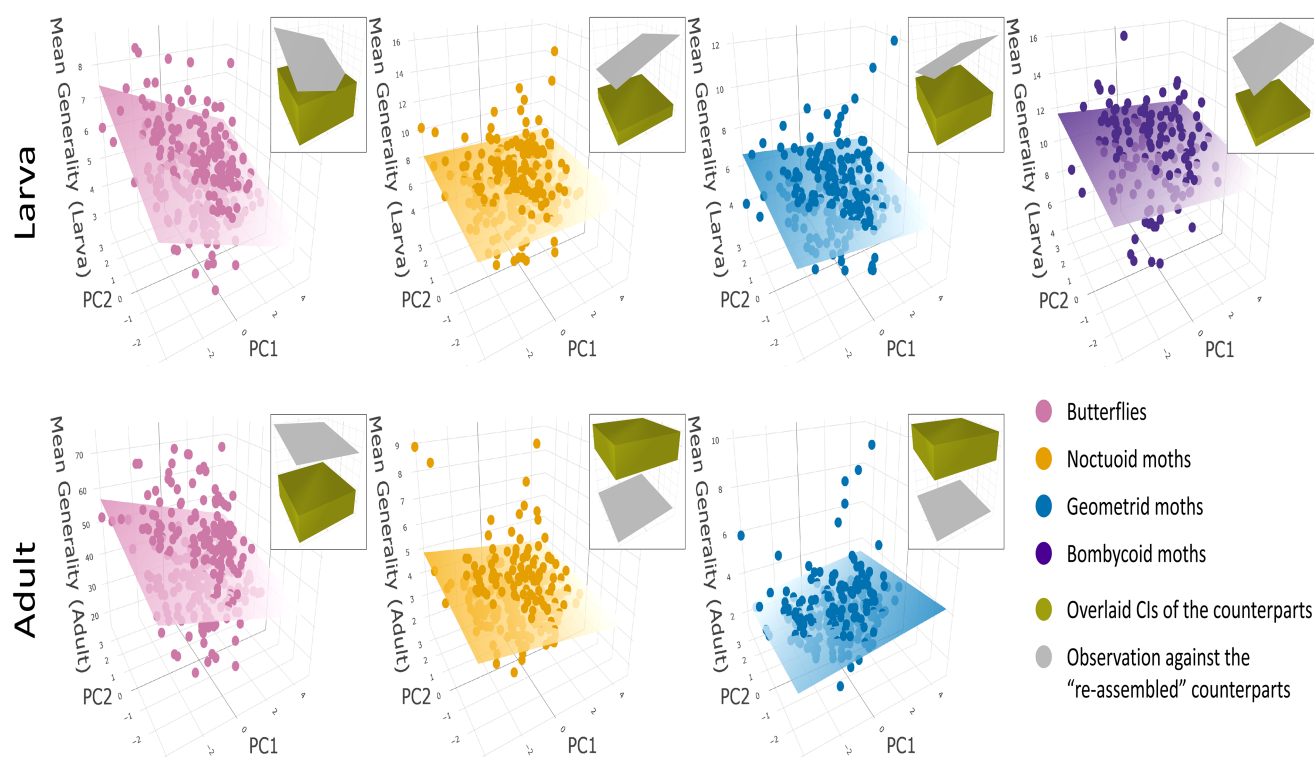


FIGURE 4 Mean generality (diet breadth) of Lepidoptera in the local networks across environmental gradients as 3D scatterplots, sharing the same environmental PC axes (as in Figure 2) but respective metric reading axis. The planes in the 3D scatterplots are regression planes of observed values, where their colour fade toward the low-value end. Corresponding stats with separated regressions against each PC are provided in Figure S9. Corresponding null-model analysis against randomised counterparts is given at each subplot's top-right; the part of the grey planes that does not overlap with the chartreuse cube (CI of the null-model counterparts) indicate where the observations are contributed by real-world species-environmental reliance (details see Section 2 and Figure 3). Note that since the total number of links, and thus mean generality, were fixed to empirical values in the 'shuffled' null model, only the 're-assembled' planes appear in the null-model analyses.

clade; Figure S12). The modularity patterns along the PC axes were inconsistent among the clades and depending on the life stage. On the one hand, the larval network of all clades tended to become less modular toward high PC2, that is increasing farm-land coverage, but only the response of butterflies was significant ($R^2=0.05$, $p<0.001$; Figure 5; Figure S12). The modularity of both Noctuid's and Geometrid's larval networks were influenced by PC1 but in opposite directions, such that the former became less modular while the latter became more modular toward high PC1, that is high elevation and low temperature ($R^2=0.01$, $p=0.062$ in Noctuid moths and $R^2=0.02$, $p=0.040$ in Geometrid moths; Figure 5; Figure S12). On the other hand, the adult networks of all clades (excl. Bombycoid moths; same for all following statements of adult-network comparisons) were influenced by PC2, such that butterflies and Noctuid moths formed less modular networks along PC2 ($R^2=0.08$, $p<0.001$ and $R^2=0.01$, $p=0.078$, respectively; Figure 5; Figure S12), while the inverse for Geometrid moths ($R^2=0.02$, $p=0.020$; Figure 5; Figure S12). Along PC1, in contrast, only Noctuid's adult networks became significantly more modular ($R^2=0.03$, $p=0.004$; Figure 5; Figure S12). The null-model analyses showed that both real-world species-environment reliance and Lepidoptera-plant interdependences (i.e., realistic lepidopteran diets) shaped network modularity in similar ways, which differed across clades and life stages. In general, these realistic biological

constraints contributed positively to the modularity of butterflies' larval networks and negatively to their adult networks, while the opposite in the moth clades (Figure 5).

As for the lepidopterans' dietary niche overlap, butterflies again had a relatively drastic divergence between life stages, as their larval diets were the least overlapped while the adult diets the most overlapped among all clades ($p<0.001$ for comparing with any moth clade; Figure S13). The environmental drivers were mostly not influential to niche overlap in larval networks. Only the diets of larval butterflies became significantly less overlapped toward high PC1 ($R^2=0.09$, $p<0.001$; Figure 6; Figure S13). On the contrary, the PCs were more influential at the adult stage. Along increasing PC1, niche overlap increased in Geometrid moths ($R^2=0.02$, $p=0.023$) but decreased in butterflies ($R^2=0.01$, $p=0.076$) and Noctuid moths ($R^2=0.07$, $p<0.001$; Figure 6; Figure S13). Along increasing PC2, diets in Noctuid and Geometrid moths' adult networks became more overlapped ($R^2=0.05$, $p<0.001$ and $R^2=0.02$, $p=0.056$, respectively; Figure 6; Figure S13). The null-model analyses again revealed consistent yet clade- and life-stage-specific contributions of both real-world species-environment reliance and Lepidoptera-plant interdependences. These constraints contributed positively to niche overlap in the larval networks of all clades, as well as in the adult networks of butterflies, while negatively in the adult networks of Geometrid moths (Figure 6).

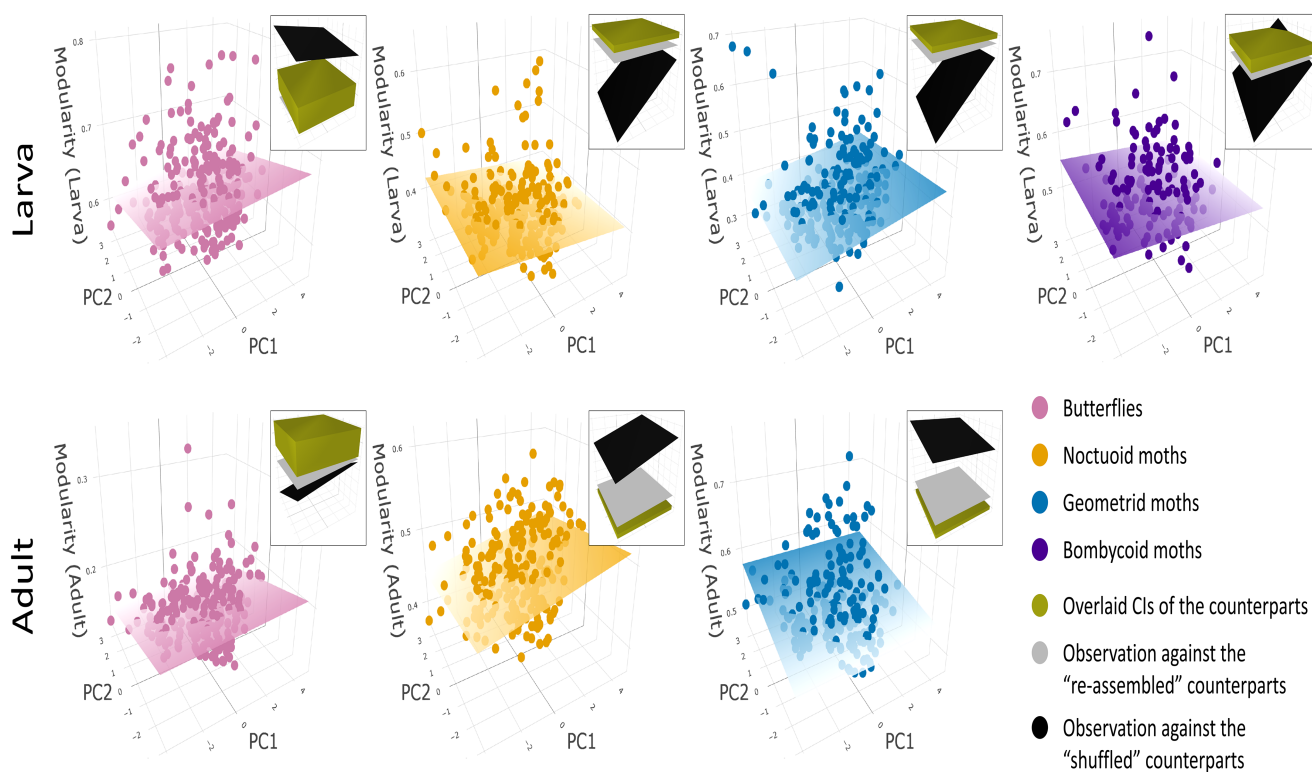


FIGURE 5 Modularity of the local networks across environmental gradients as 3D scatterplots, sharing the same environmental PC axes (as in Figure 2) but respective metric reading axis. The planes in the 3D scatterplots are regression planes of observed values, where their colour fade toward the low-value end. Corresponding stats with separated regressions against each PC are provided in Figure S10. Corresponding null-model analysis against randomised counterparts is given at each subplot's top-right; the part of the grey/black planes that does not overlap with the chartreuse cube (CI of the null-model counterparts) indicate where the observed values are contributed by real-world species-environmental reliance/Lepidoptera-plant interdependences, respectively (details see Section 2 and Figure 3).

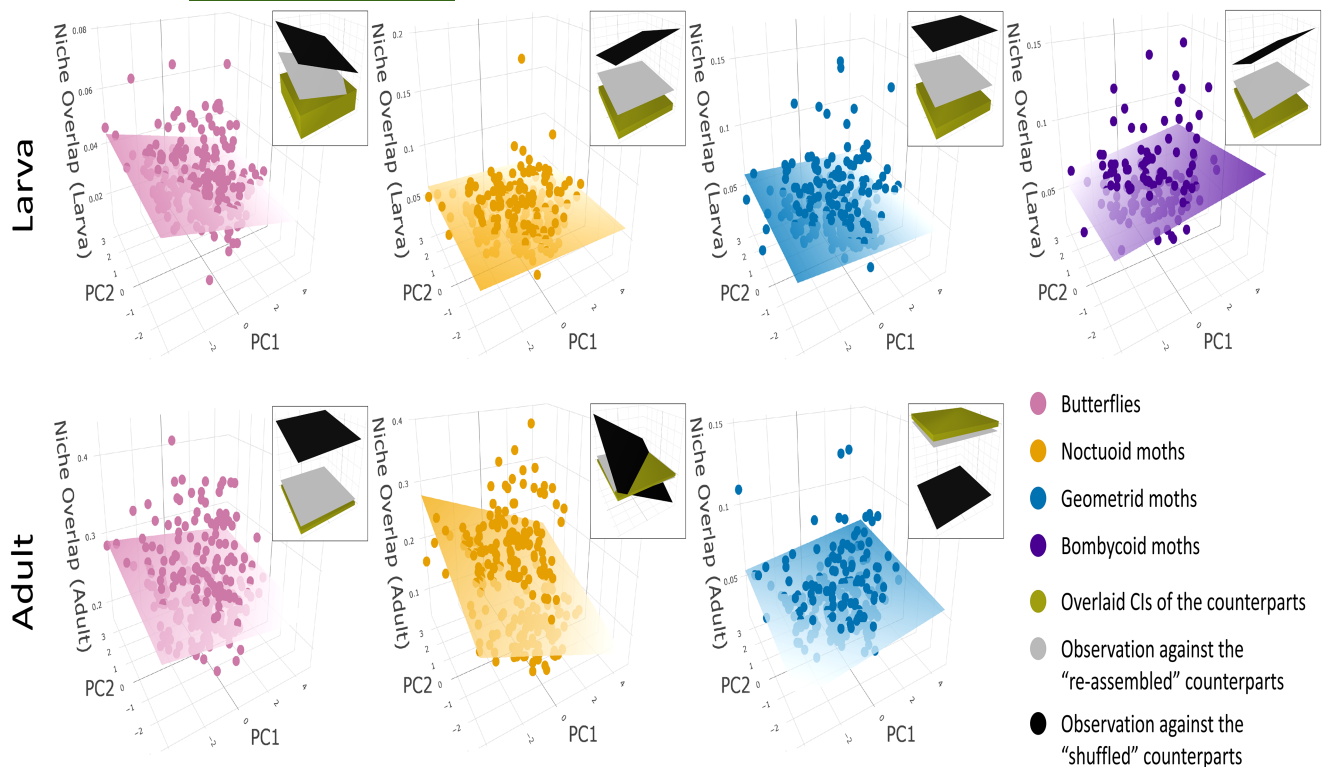


FIGURE 6 Dietary niche overlap of Lepidoptera in the local networks across environmental gradients as 3D scatterplots, sharing the same environmental PC axes (as in Figure 2) but respective metric reading axis. The planes in the 3D scatterplots are regression planes of observed values, where their colour fade toward the low-value end. Corresponding stats with separated regressions against each PC are provided in Figure S11. Corresponding null-model analysis against randomised counterparts is given at each subplot's top-right; the part of the grey/black planes that does not overlap with the chartreuse cube (CI of the null-model counterparts) indicate where the observed values are contributed by real-world species-environmental reliance/Lepidoptera-plant interdependences, respectively (details see Section 2 and Figure 3).

4 | DISCUSSION

Based on extensive datasets of species occurrences and interactions, we brought together biogeographic and ecological knowledge to reveal landscape-scale spatial patterns of species diversity and potential interaction networks of Lepidoptera-plant communities. Specifically, these patterns reveal how abiotic (e.g., climate and land cover) and biotic (e.g., resource-consumer reliance) factors may together determine the composition and structure of local interaction networks. Overall, local Lepidoptera richness, regardless of clades, positively correlated with plant richness. Meanwhile, network structural metrics did not exhibit identical spatial patterns (along PC1 and PC2) as those of Lepidoptera richness, even when clades and life stages are looked at individually. We therefore found no support for our first hypothesis that environmental conditions unfavourable to biodiversity also bring about simpler network structure. Actually, the effects of environmental drivers on Lepidoptera richness were not universal either, as different clades showed different richness patterns along the PCs. Yet, as secondly hypothesised, we saw divergent spatial-structural patterns among Lepidoptera clades (often between butterflies and moths) and between life stages. The goodness of fit of our regression models (R^2) were comparable to those of other studies adopting similar approaches and looking at

properties of similar-sized networks along gradients (Ho et al., 2022; also Section S1). Below we mainly discuss the detected patterns, whereas an extended discussion on others is in Section S1.

The richness patterns likely reflect Lepidoptera's dependence on their interacting plants rather than the reverse, given that most lepidopterans across life stages are sole and relatively specialised plant feeders (Pearse & Altermatt, 2013a), while plants rarely rely only on Lepidoptera adults to pollinate them (Gibson et al., 2006; Memmott, 1999). Thus, more diverse local plant assemblages can potentially support the existence of more Lepidoptera species (Axmacher et al., 2009). This was supported, yet only weakly, by our richness correlation analyses (Figure S2), suggesting that Lepidoptera richness is not only constrained by food-plant diversity. Indeed, we detected systematic difference in spatial diversity patterns among Lepidoptera clades, such that butterfly richness was driven more by geo-climatic environmental factors (PC1; more diverse toward higher elevation), while the richness of the moth clades more by land covers (PC2; more diverse toward farmland-dominant lands). Our butterfly altitudinal richness pattern echoes other butterfly studies in nearby geographical regions and likely captures the positive richness-elevation association before reaching a mid-elevation (~1,500 m a.s.l.) peak or plateau (see dome-shape relationships observed in Gallou et al., 2017; Ho et al., 2022). Since

this pattern was butterfly-specific, it is unlikely shaped by geometric 'spurious Rapoport effect' (caused by non-biological sampling bias, see Colwell & Hurr, 1994) that would have prevailed also in other clades, but instead reflecting biological constraints. Such constraints should not be altitudinal food-plant diversity variation either, as plant richness actually decreased with our PC1 in the study area (Figure 1; Figure S14). Thus, it is possible that certain non-food habitat properties co-varying with elevation, for example higher microhabitat variability (Figure S15) or less-intense agriculture (with which our PC2 accounting only land cover could not fully capture), are important especially to butterflies and thus drive their local richness (Hill et al., 2021; Kleckova et al., 2014; Maes & Van Dyck, 2001). Conversely, for moths, food-plant diversity may be a relatively more-influential driver, as we saw congruently that plant richness increased with our PC2 (Figure 1). Agricultural land use may have created heterogeneous habitats at the cell scale we looked at, thereby supporting more diverse local food plants.

Regarding the potential diets of Lepidoptera across all constructed local networks, butterflies generally had narrower diets than the moths as larvae, but broader ones as adults. Note that these locally realised diets were determined by both the lepidopterans' diet breadths (feeding habits) and the local availabilities of food plants. We conducted a further comparison between butterflies' and moths' diets within our metawebs, that is accounting for only their diet breadths, and found consistent patterns (Figure S16). Therefore, these patterns mainly mirrored diet-breadth difference among Lepidoptera clades. Butterfly larvae may experience comparatively stronger food-plant competition or predation, under which conditions a narrower diet would be favoured (Dyer, 1995; Wiklund & Friberg, 2008). Meanwhile, butterfly adults tend to be more-generalist nectar feeders than moths, likely also because there are more plants flowering during the day than at night (Borges et al., 2016). This has provided a broader spectrum of potential resources allowing the diurnal butterflies to evolve for adult food usage, whereas the fewer night-flowering plants and nocturnal moths have to evolve toward tighter mutual dependence. We also note that the strict diurnal vs. nocturnal active patterns between butterflies and moths, particularly at the adult stage, may have led to an underestimation of moths' diets because observing their interactions with flowers is intrinsically more difficult in the dark. Nonetheless, since there is no systematic sampling bias expected along environmental gradients, the spatial patterns of Lepidoptera diet breadths (as well as of other metrics) should be realistic.

In general, local potential diet breadth of most Lepidoptera clades across their life stages tended to become broader toward low-elevation farmlands (low PC1 and high PC2), possibly because of more diverse plants in such habitats (Figure 1) presenting more food plants to co-occur with the Lepidoptera. However, we cannot rule out that such local conditions (more-perturbed farmlands) may favour the existence of generalist over specialist consumers (Büchi & Vuilleumier, 2014). An interesting exception was the adults of Geometrid moths, whose potential diets statistically broadened toward high-elevation forests (high PC1 and low PC2), countering

the trend of local plant richness. It is possible that such conditions favour more-generalist Geometrids, driven by weaker plant resistance or other factors as reported in other plant-feeding insects (Moreira et al., 2018; Pellissier et al., 2012). However, given the reported Geometrids' adult diets are narrow (Figure S11), such trends were relatively trivial. The lepidopterans' local diet breadths were broader in observed communities than in randomly re-assembled ones across clades and life stages, except for adult Noctuid and Geometrid moths. The former pattern suggests that generalist Lepidoptera are relatively widespread (thus, per-cell re-assembling undersamples these generalists and leads to narrower diets), but this is less effective for adult moths who, despite variation in diet breadths, are generally narrow feeders. Relatively-generalist adult moths may be spatially restricted, or local plant assemblage tends to contain only a minor fraction of their food plants due to pollinator competition (thus per-cell re-assembling oversamples the generalists or their food plants and lead to broader diets). The latter condition could be shaped by pollinator competition among plants.

Network modularity is typical in plant-herbivore and (large) plant-pollinator networks (Olesen et al., 2007; Thébaud & Fontaine, 2010), including those of Lepidoptera larvae and adults (Astegiano et al., 2017). Our results showed that butterflies' larval networks were more modular than those of the moth clades, yet the opposite for adult networks (Figure S12). Part of such butterfly-moth difference should associate with their diet-breadth difference as addressed above. As for butterflies, their diurnal adults interact with diverse flowering plants, and their nectar feeding is benefiting the plants with pollination functions. Under such conditions, evolution with plants would favour butterfly adults to feed on non-specialised, diverse nectars, thereby suppressing the formation of network modularity. Compared to the adults that can fly to access alternative nectar sources, their larvae are relatively immobile and thus need to be able to well-consume the individual host plant that they settle on. The larval evolutionary arm race with the host plants should consequently favour phylogenetically or physiologically conservative diets (Futuyma & Moreno, 1988), thereby making modularity prevail in larval networks (Figure S12; Andreazzi et al., 2017). Such inferences are congruent with our null-model analyses, such that real-world Lepidoptera-plant interdependences (realistic butterfly diets) positively contributed to modularity in butterflies' larval networks yet negatively in adult ones. As for moths, their adult networks were more modular than either type of null-model counterparts. This suggests a tighter evolution with plants particularly in their adult phase, which is reasonable, given nocturnal flowering plants are way fewer than diurnal ones.

As dietary modules within networks often emerge from narrow and specialised diets (Tim Tinker et al., 2012), it is expectable that the spatial-modularity patterns of Lepidoptera-plant networks should generally counter their spatial-generalist patterns, which we indeed observed (Figures 4 and 5; Figures S9 and S10). On top of such associations, there are also mechanisms that can contribute to the formation of varying modularity along environmental gradients. For example, the modularity of larval and adult butterfly networks

was both negatively associated with farmland coverage (PC2), possibly due to anthropogenic influences. Agriculture modifies species composition of local communities to deviate from their phylogenetic structure or co-evolutionary legacy shaped before perturbation (Moora et al., 2014; Toyama et al., 2015), thereby mitigating the emergent network modularity. Consistently, as shown by null-model analyses, real-world species-environment reliance contributed negatively to butterfly networks' modularity across life stages (more pronounced in adult ones) particularly toward high PC2. Meanwhile, the modularity of larval networks of Noctuid moths associated negatively with PC1. This pattern may reflect relatively more-effective local competitive exclusions toward high elevations (possible mechanisms see Montaña-Centellas et al., 2021), such that larvae sharing similar food plants (belonging to the same interaction module) tend not to co-occur.

In terms of potential dietary niche overlap in local networks, butterfly larvae had the lowest, while adults the highest, overlap among all clades. This echoes our above reasoning of diet specialisation of butterfly larvae vs. adults, as the same mechanisms lead also to differentiated diets among species. With larval networks, the environmental gradients were generally not influential to lepidopterans' niche overlap, while only butterfly larvae's diets became less overlapped with PC1. Interestingly, if without other constraints, butterflies' diets should passively become more overlapped given that their richness increases while plant richness decreases along PC1. Thus, such an inverse trend in larval networks suggests a compositional shift toward dietary more-differentiated butterfly larvae at higher elevations (Pellissier et al., 2012), which may have suppressed their diet breadth in addition to the effect of fewer food plants available. Contrastingly, environmental gradients were relatively influential to niche overlap in adult networks. The overlap tended to be higher toward low-elevation farmlands (low PC1 and high PC2) with butterflies and Noctuid moths, while toward high-elevation farmlands (high PC1 and PC2) with Geometrid moths, though the latter was relatively trivial. These patterns largely echo those of diet breadths and may be associated with the spatial pattern of plant richness, or the environmental conditions favouring dietary generalists over specialists. Given the particularly narrow diets of adult Geometrid moths, diet differentiation should be important for those locally coexisting. This is supported by that they adopted the lowest niche overlap among clades, and null models indicated that real-world constraints contributed negatively to their niche overlap.

By addressing the geo-climate and land-cover relevance of landscape-scale Lepidoptera-plant networks, we revealed across Lepidoptera clades and life stages how their (co-)evolved traits (e.g., diet breadth), interaction types (antagonistic vs. mutualistic; see Thébaud & Fontaine, 2010), and ecological relationships with others (e.g., resource competition, local food availability) collectively drive different interaction structures in response to environmental variations. Such biogeographical understandings of interaction networks may provide conservation implications as the Lepidoptera in Baden-Württemberg are declining (Habel et al., 2019; Karbiener & Trusch, 2022). For example, given that networks with high dietary

overlap are generally more vulnerable to food plant loss, whereas those with low modularity are sensitive to cascading harmful perturbations (Pires et al., 2020; Stouffer & Bascompte, 2011), our results indicate specific lepidopteran clade(s) and habitat type(s) that may worth prioritised concerns. Moreover, the detected spatial patterns can inform how these communities tend to react to potential environmental changes caused by anthropogenic land use or climate change (Hill et al., 2021; Ho et al., 2022). While here we compared Lepidoptera clades and life stages separately, in reality, they harbour in the same communities and influence each other simultaneously. A taxonomically integrated revisit would be promising to provide insights into the intertwined dynamics of Lepidoptera-plant communities.

ACKNOWLEDGEMENTS

We thank all the many people who collected the occurrence data of Lepidoptera and plants upon which our analyses are based on. Without their naturalist skills and efforts, such analyses would simply not be possible. We specifically thank Robert Trusch and Arno Wörz (both Staatliches Museum für Naturkunde Stuttgart) for providing access to the Lepidoptera and plant data, respectively. We thank Rosi Siber for extracting needed GIS data. No field work permits were required in our study, and we based all analyses on existing databases and publications that we specifically referred to and acknowledged. Funding is through the University of Zurich Research Priority Program in Global Change and Biodiversity (URPP GCB) as well as the Swiss National Science Foundation (Grant Nr. 310030_197410) to FA. HH is supported by the Yushan Young Fellow program, MOE, Taiwan.

CONFLICT OF INTEREST STATEMENT

The authors claim no competing interest.

DATA AVAILABILITY STATEMENT

The Lepidoptera and plant occurrence data can be obtained at *Database Arbeitsgruppe Schmetterlinge Baden-Württembergs*, *Bundesamt für Naturschutz*, and *Floraweb*, respectively. The GIS data can be derived from corresponding databases (see Section 2). The compiled metawebs can be accessed upon request to FA. The processed local network data, as well as the R codes that reproduce all analyses and figures in this study, are provided at <https://doi.org/10.6084/m9.figshare.24557725.v1>.

ORCID

Hsi-Cheng Ho  <https://orcid.org/0000-0002-0734-0249>

Florian Altermatt  <https://orcid.org/0000-0002-4831-6958>

REFERENCES

- Altermatt, F., & Pearse, I. S. (2011). Similarity and specialization of the larval versus adult diet of European butterflies and moths. *The American Naturalist*, 178(3), 372–382.
- Andreazzi, C. S., Thompson, J. N., & Guimarães, P. R., Jr. (2017). Network structure and selection asymmetry drive coevolution in species-rich antagonistic interactions. *The American Naturalist*, 190(1), 99–115.

- Astegiano, J., Altermatt, F., & Massol, F. (2017). Disentangling the co-structure of multilayer interaction networks: Degree distribution and module composition in two-layer bipartite networks. *Scientific Reports*, 7(1), 1–11.
- Axmacher, J. C., Brehm, G., Hemp, A., Tünste, H., Lyaruu, H. V., Müller-Hohenstein, K., & Fiedler, K. (2009). Determinants of diversity in afrotropical herbivorous insects (Lepidoptera: Geometridae): Plant diversity, vegetation structure or abiotic factors? *Journal of Biogeography*, 36(2), 337–349.
- Bascompte, J. (2009). Disentangling the web of life. *Science*, 325(5939), 416–419.
- Boggs, C. L. (1987). Ecology of nectar and pollen feeding in Lepidoptera. In F. Slansky Jr., and J. G. Rodriguez (Eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*. (pp. 369–391). New York: John Wiley.
- Borges, R. M., Somanathan, H., & Kelber, A. (2016). Patterns and processes in nocturnal and crepuscular pollination services. *The Quarterly Review of Biology*, 91(4), 389–418.
- Braga, M. P., Guimarães, P. R., Wheat, C. W., Nylin, S., & Janz, N. (2018). Unifying host-associated diversification processes using butterfly-plant networks. *Nature Communications*, 9(1), 1–10.
- Büchi, L., & Vuilleumier, S. (2014). Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. *The American Naturalist*, 183(5), 612–624.
- Carvajal Acosta, A. N., & Mooney, K. (2021). Effects of geographic variation in host plant resources for a specialist herbivore's contemporary and future distribution. *Ecosphere*, 12(11), e03822.
- Colwell, R. K., & Hurltt, G. C. (1994). Nonbiological gradients in species richness and a spurious Rapoport effect. *The American Naturalist*, 144(4), 570–595.
- Després, L., David, J. P., & Gallet, C. (2007). The evolutionary ecology of insect resistance to plant chemicals. *Trends in Ecology & Evolution*, 22(6), 298–307.
- Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal*, 2(1), 7–24.
- Dyer, L. A. (1995). Tasty generalists and nasty specialists? Antipredator mechanisms in tropical lepidopteran larvae. *Ecology*, 76(5), 1483–1496.
- Ebert, G. (1991–2005). *Die Schmetterlinge Baden-Württembergs* (Vol. 1–10). Ulmer.
- Frelat, R., Kortsch, S., Kröncke, I., Neumann, H., Nordström, M. C., Olivier, P. E., & Sell, A. F. (2022). Food web structure and community composition: A comparison across space and time in the North Sea. *Ecography*, 2022(2), e05945.
- Futuyma, D. J., & Moreno, G. (1988). The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, 19, 207–233.
- Gallou, A., Baillet, Y., Ficetola, G. F., & Després, L. (2017). Elevational gradient and human effects on butterfly species richness in the French Alps. *Ecology and Evolution*, 7(11), 3672–3681.
- Gibson, R. H., Nelson, I. L., Hopkins, G. W., Hamlett, B. J., & Memmott, J. (2006). Pollinator webs, plant communities and the conservation of rare plants: Arable weeds as a case study. *Journal of Applied Ecology*, 43(2), 246–257.
- Habel, J. C., Trusch, R., Schmitt, T., Ochse, M., & Ulrich, W. (2019). Long-term large-scale decline in relative abundances of butterfly and burnet moth species across South-Western Germany. *Scientific Reports*, 9(1), 1–9.
- Hanspach, J., Schweiger, O., Kühn, I., Plattner, M., Pearman, P. B., Zimmermann, N. E., & Settele, J. (2014). Host plant availability potentially limits butterfly distributions under cold environmental conditions. *Ecography*, 37(3), 301–308.
- Hill, G. M., Kawahara, A. Y., Daniels, J. C., Bateman, C. C., & Scheffers, B. R. (2021). Climate change effects on animal ecology: Butterflies and moths as a case study. *Biological Reviews*, 96(5), 2113–2126.
- Ho, H. C., Brodersen, J., Gossner, M. M., Graham, C. H., Kaeser, S., Chacko, M. R., Seehausen, O., Zimmermann, N. E., Pellissier, L., & Altermatt, F. (2022). Blue and green food webs respond differently to elevation and land use. *Nature Communications*, 13(1), 6415.
- Jones, J. P. (2011). Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology*, 48(1), 9–13.
- Karbiener, O., & Trusch, R. (2022). *Wandel der Nachtfalterfauna Baden-Württembergs seit 1970*. Staatliches Museum für Naturkunde.
- Kehoe, R., Frago, E., & Sanders, D. (2021). Cascading extinctions as a hidden driver of insect decline. *Ecological Entomology*, 46(4), 743–756.
- Kleckova, I., Konvicka, M., & Klecka, J. (2014). Thermoregulation and microhabitat use in mountain butterflies of the genus *Erebia*: Importance of fine-scale habitat heterogeneity. *Journal of Thermal Biology*, 41, 50–58.
- Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., & Planque, B. (2019). Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography*, 42(2), 295–308.
- Lau, D. C., Christoffersen, K. S., Erkinaro, J., Hayden, B., Heino, J., Hellsten, S., Holmgren, K., Kahilainen, K. K., Kahlert, M., Karjalainen, S. M., Karlsson, J., Forsström, L., Lento, J., Mjelde, M., Ruuhijärvi, J., Sandøy, S., Schartau, A. K., Svenning, M.-A., Vrede, T., & Goedkoop, W. (2022). Multitrophic biodiversity patterns and environmental descriptors of sub-Arctic lakes in northern Europe. *Freshwater Biology*, 67(1), 30–48.
- Liu, H., Liu, Z., Zhang, M., Bascompte, J., He, F., & Chu, C. (2021). Geographic variation in the robustness of pollination networks is mediated by modularity. *Global Ecology and Biogeography*, 30(7), 1447–1460.
- López-Carretero, A., Díaz-Castelazo, C., Boege, K., & Rico-Gray, V. (2014). Evaluating the spatio-temporal factors that structure network parameters of plant-herbivore interactions. *PLoS One*, 9(10), e110430.
- Losapio, G., Jordán, F., Caccianiga, M., & Gobbi, M. (2015). Structure-dynamic relationship of plant-insect networks along a primary succession gradient on a glacier foreland. *Ecological Modelling*, 314, 73–79.
- Maes, D., & Van Dyck, H. (2001). Butterfly diversity loss in Flanders (North Belgium): Europe's worst case scenario? *Biological Conservation*, 99(3), 263–276.
- Mantyka-Pringle, C. S., Visconti, P., Di Marco, M., Martin, T. G., Rondinini, C., & Rhodes, J. R. (2015). Climate change modifies risk of global biodiversity loss due to land-cover change. *Biological Conservation*, 187, 103–111.
- Martins, L. P., Stouffer, D. B., Blendinger, P. G., Böhning-Gaese, K., Buitrón-Jurado, G., Correia, M., Costa, J. M., Dehling, D. M., Donatti, C. I., Emer, C., Galetti, M., Heleno, R., Jordano, P., Menezes, Í., Morante-Filho, J. C., Muñoz, M. C., Neuschulz, E. L., Pizo, M. A., Quitián, M., ... Tylianakis, J. M. (2022). Global and regional ecological boundaries explain abrupt spatial discontinuities in avian frugivory interactions. *Nature Communications*, 13(1), 6943.
- Memmott, J. (1999). The structure of a plant-pollinator food web. *Ecology Letters*, 2(5), 276–280.
- Montaño-Centellas, F. A., Loiselle, B. A., & Tingley, M. W. (2021). Ecological drivers of avian community assembly along a tropical elevation gradient. *Ecography*, 44(4), 574–588.
- Moora, M., Davison, J., Öpik, M., Metsis, M., Saks, Ü., Jairus, T., Vasar, M., & Zobel, M. (2014). Anthropogenic land use shapes the composition and phylogenetic structure of soil arbuscular mycorrhizal fungal communities. *FEMS Microbiology Ecology*, 90(3), 609–621.
- Moreira, X., Petry, W. K., Mooney, K. A., Rasmann, S., & Abdala-Roberts, L. (2018). Elevational gradients in plant defences and insect herbivory: Recent advances in the field and prospects for future research. *Ecography*, 41(9), 1485–1496.
- Muto-Fujita, A., Takemoto, K., Kanaya, S., Nakazato, T., Tokimatsu, T., Matsumoto, N., Kono, M., Chubachi, Y., Ozaki, K., & Kotera, M.

- (2017). Data integration aids understanding of butterfly–Host plant networks. *Scientific Reports*, 7(1), 1–14.
- Narango, D. L., Tallamy, D. W., & Shropshire, K. J. (2020). Few keystone plant genera support the majority of Lepidoptera species. *Nature Communications*, 11(1), 1–8.
- Neff, F., Brändle, M., Ambarli, D., Ammer, C., Bauhus, J., Boch, S., Hölzel, N., Klaus, V. H., Kleinebecker, T., Prati, D., Schall, P., Schäfer, D., Schulze, E. D., Seibold, S., Simons, N. K., Weisser, W. W., Pellissier, L., & Gossner, M. M. (2021). Changes in plant–herbivore network structure and robustness along land-use intensity gradients in grasslands and forests. *Science Advances*, 7(20), eabf3985.
- Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences*, 104(50), 19891–19896.
- Pearse, I. S., & Altermatt, F. (2013a). Predicting novel trophic interactions in a non-native world. *Ecology Letters*, 16(8), 1088–1094.
- Pearse, I. S., & Altermatt, F. (2013b). Extinction cascades partially estimate herbivore losses in a complete Lepidoptera–plant food web. *Ecology*, 94(8), 1785–1794.
- Pearse, I. S., & Altermatt, F. (2015). Out-of-sample predictions from plant–insect food webs: Robustness to missing and erroneous trophic interaction records. *Ecological Applications*, 25(7), 1953–1961.
- Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M. A., Melián, C. J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N. E., & Gravel, D. (2018). Comparing species interaction networks along environmental gradients. *Biological Reviews*, 93(2), 785–800.
- Pellissier, L., Fiedler, K., Ndrube, C., Dubuis, A., Pradervand, J. N., Guisan, A., & Rasmann, S. (2012). Shifts in species richness, herbivore specialization, and plant resistance along elevation gradients. *Ecology and Evolution*, 2(8), 1818–1825.
- Pires, M. M., O'Donnell, J. L., Burkle, L. A., Díaz-Castelazo, C., Hembry, D. H., Yeakel, J. D., Newman, E. A., Medeiros, L. P., de Aguiar, M. A. M., & Guimarães, P. R., Jr. (2020). The indirect paths to cascading effects of extinctions in mutualistic networks. *Ecology*, 101, e03080.
- Poisot, T., Canard, E., Mouillot, D., Mouquet, N., & Gravel, D. (2012). The dissimilarity of species interaction networks. *Ecology Letters*, 15(12), 1353–1361.
- R Core Team. (2013). R: A language and environment for statistical computing.
- Saravia, L. A., Marina, T. I., Kristensen, N. P., De Troch, M., & Momo, F. R. (2022). Ecological network assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91(3), 630–642.
- Scoble, M. J. (1995). *The Lepidoptera. Form, function and diversity*. Oxford University Press.
- Stouffer, D. B., & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences*, 108(9), 3648–3652.
- Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329(5993), 853–856.
- Thompson, R. M., Brose, U., Dunne, J. A., Hall, R. O., Jr., Hladyz, S., Kitching, R. L., Martinez, N. D., Rantala, H., Romanuk, T. N., Stouffer, D. B., & Tylianakis, J. M. (2012). Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, 27(12), 689–697.
- Tim Tinker, M., Guimaraes, P. R., Jr., Novak, M., Marquitti, F. M. D., Bodkin, J. L., Staedler, M., Bentall, G., & Estes, J. A. (2012). Structure and mechanism of diet specialisation: Testing models of individual variation in resource use with sea otters. *Ecology Letters*, 15(5), 475–483.
- Toyama, H., Kajisa, T., Tagane, S., Mase, K., Chhang, P., Samreth, V., Ma, V., Sokh, H., Ichihashi, R., Onoda, Y., Mizoue, N., & Yahara, T. (2015). Effects of logging and recruitment on community phylogenetic structure in 32 permanent forest plots of Kampong Thom, Cambodia. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 370(1662), 20140008.
- Tylianakis, J. M., Laliberté, E., Nielsen, A., & Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation*, 143(10), 2270–2279.
- Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, 48, 25–48.
- Tylianakis, J. M., Tscharntke, T., & Lewis, O. T. (2007). Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, 445(7124), 202–205.
- Weiblen, G. D., Webb, C. O., Novotny, V., Basset, Y., & Miller, S. E. (2006). Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology*, 87(sp7), S62–S75.
- White, J. W., Rassweiler, A., Samhouri, J. F., Stier, A. C., & White, C. (2014). Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos*, 123(4), 385–388.
- Wiklund, C., & Friberg, M. (2008). Enemy-free space and habitat-specific host specialization in a butterfly. *Oecologia*, 157(2), 287–294.
- Woodward, G., & Hildrew, A. G. (2002). Food web structure in riverine landscapes. *Freshwater Biology*, 47(4), 777–798.

BIOSKETCH

Hsi-Cheng Ho is interested in linking animal behaviour to community-level ecological phenomena, especially ecological networks' properties.

Florian Altermatt is interested in linking community ecology processes, such as species interactions and dispersal, with biodiversity and ecosystem functioning at larger, regional scales. FA is also a keen naturalist of Lepidoptera and their ecology.

Author contributions: Florian Altermatt conceived the idea and developed it into a project together with Hsi-Cheng Ho. Florian Altermatt secured the funding. Florian Altermatt compiled the primary data and Hsi-Cheng Ho designed and performed the analyses. Hsi-Cheng Ho led the writing with consistent and significant input from Florian Altermatt.

SUPPORTING INFORMATION

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

How to cite this article: Ho, H.-C., & Altermatt, F. (2023). Associating the structure of Lepidoptera–plant interaction networks across clades and life stages to environmental gradients. *Journal of Biogeography*, 00, 1–14. <https://doi.org/10.1111/jbi.14776>