



Research Paper

The relationship between plant and butterfly biodiversity is altered by compound effects of human activities at landscape and regional scales

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ABSTRACT

Understanding how human activities influence biodiversity is a pressing challenge. Here, we ask whether obligate biotic interactions between plants and butterflies respond to patterns in anthropogenic disturbance at landscape and regional scales. Here, we used hierarchical models to understand how the relationships between alpha and beta taxonomic diversities of butterflies and plants change across landscapes and regions exposed to a gradient of anthropogenic influence.

Analyzing 1682 sampling sites in which butterfly and plant species were both inventoried, from 45 studies identified through a literature review, we found that ecological communities sampled in highly disturbed areas displayed a lower number of butterfly species per plant species, and more homogenized butterfly communities. These responses were exacerbated when human activities affected both the landscape and the region hosting the plant and butterfly communities assessed.

Our results suggest that human activities can differentially affect butterflies and plants, two co-evolved groups, thus altering long-term eco-evolutionary dynamics. They also hint at how the negative effects of human activities on biodiversity compound between landscape and regional scales, illustrating the importance of multi-scale analyses and approaches for understanding and protecting biodiversity globally.

Introduction

Global biodiversity loss is considered one of the most dangerous ongoing anthropogenic trends for human societies (Rockström et al., 2023). Because human populations have already affected large areas of the planet, often resulting in different types of pressures that overlap and potentially interact (Bowler et al., 2020), conservation scientists are investing considerable resources in understanding how different taxa are responding to global change drivers (Jaureguiberry et al., 2022; Newbold et al., 2015). In this context, several studies demonstrate that human activities can profoundly affect the composition of ecological communities across space and through time (Dornelas et al., 2019; Newbold et al., 2015; Riva & Fahrig, 2023). Yet, how human activities

affect species interactions has received less attention than other biodiversity facets (Caron et al., 2024; Heinen et al., 2020; Pollock et al., 2020).

Among several types of ecological interactions, obligate interactions where one taxon necessarily rely on the presence of another for its survival are of particular conservation interest (Hembry & Weber, 2020; Nakazawa, 2020). This is because the disruption of such obligate interactions can affect ecosystems via potential “secondary” or “cascading” extinctions (Brodie et al., 2014; Colwell et al., 2012). Understanding obligate biotic interactions is therefore essential for biodiversity conservation, yet our understanding of how taxa involved in these relationships conjunctly respond to global change remains very limited (Colwell et al., 2012; Heinen et al., 2020), contributing to the

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“Eltonian shortfall” (Hortal et al., 2015). Notably, this lack of knowledge on biotic interactions is intertwined with a limited understanding of how biodiversity changes across spatial scales (Riva & Fahrig, 2023; Riva et al., 2024b).

One of the most iconic examples of obligate biotic interactions are the trophic relationships between plants and butterflies (Ehrlich & Raven, 1964). Butterflies coevolved with plants for millions of years, such that most butterfly caterpillars must feed on one or a few specific host plant families to survive (Braby & Trueman, 2006; Ehrlich & Raven, 1964; Kawahara et al., 2023). When human activities cause the extinction of the larval host plants of a butterfly species, the butterfly species typically also disappears (Descombes et al., 2016). This link is captured by the well-established positive relationship between the diversity of plants and butterflies (Ebeling et al., 2008; Hawkins & Porter, 2003). Indeed, the positive relationship between plant and butterfly species richness is a nearly universal pattern that clearly emerges due to this strong trophic relationship (Castagneyrol & Jactel, 2012).

The positive relationship between butterfly and plant diversity is a specific case of more broadly studied relationships between plant diversity and the diversity of several other taxa. Many studies have demonstrated strong relationships between plant species richness and the richness of animal taxa (Castagneyrol & Jactel, 2012; Lewinsohn & Roslin, 2008), including arthropods that relate to plants across different trophic levels (Holmes & Blubaugh, 2023), such as pollinators (Kral-O'Brien et al., 2021). The relationship between butterfly and plant diversity, however, is of particular interest because butterflies inherently depend on plants for their life cycle. Despite several case studies showing strong positive correlations in biodiversity between plants and butterflies (Hawkins and Porter, 2003), including cases demonstrating that human activities affect this relationship (Riva et al., 2020), a synthesis of how these two groups respond jointly to human activities is, to date, missing in the literature.

Here, we synthesize data from 45 studies and 1682 sampling locations where the species richness of butterflies and plants were documented to test hypotheses on how human activities at landscape and regional scales influence the relationship between plant and butterfly biodiversity. Specifically, we regressed butterfly alpha (i.e., species richness) and beta (i.e., the proportion of species found at the site-level) taxonomic diversities on plant alpha and beta diversities, while accounting for (i) whether the landscapes assessed were dominated by anthropogenic land cover types (i.e., semi-natural vs. human dominated landscapes) and (ii) whether the studies were located in highly disturbed regions, as approximated by the Human Footprint Index (HFI) (J.A. Venter et al., 2016).

While alpha and beta diversities of plants and butterflies are well-known to be positively related (Castagneyrol and Jactel, 2012; Kral-O'Brien et al., 2021), our focus here is on understanding the degree to which this positive relationship might change with human activities at landscape and regional scales. The most parsimonious expectation for these relationships is that, while human activities might reduce both plant and butterfly richness across a group of sites, the relationship between plant and butterfly diversity would not change because both butterflies and plants would suffer equally from human activities. For instance, when considering taxonomic alpha diversity, the total number of butterflies observed per plant species would remain constant across studies (i.e., a stable ratio of butterfly species per plant species with increasing disturbance). In this case, both taxa would suffer from biodiversity loss due to human activities [e.g., habitat loss; (Riva et al., 2024a)], but the slopes of these relationships would not change. Alternatively, human activities might influence these relationships, e.g., the slope steepness of the taxonomic alpha diversity relationship could (i) increase when a higher number of plant species than butterfly species is lost in comparison to undisturbed conditions, or (ii) decrease when a higher number of butterfly species than plant species is lost in comparison to undisturbed conditions. Such effects might occur due to

landscape-scale disturbances, regional-scale disturbances, or both.

Material & methods

Data gathering

We started by designing a systematic literature review to gather data on plant and butterfly species richness across multiple studies. We used the “Web Of Science Core Collection” (WoS) platform, accessed from University of Lausanne to gather data on plant and butterfly richness estimates from 1900 to May 12, 2023. We used the following formula: (ALL=(butterfl*) OR ALL=(Rhopalocera)) AND (ALL=(plant*) OR ALL=(angiosperm*)) AND (ALL=(species richness) OR ALL=(biodiversity)), which returned 1714 papers. We then randomly checked 650 papers. We deemed this sample (~38% of the literature) reasonable to address our research questions, because we could not review all 1714 papers due to limited resources. We applied inclusion criteria for the evaluation of papers relevant to our study design (Grames & Elphick, 2020; Pullin & Stewart, 2006), discarding studies where (i) the diversity of plant and butterfly species was limited to a subset of species (e.g., only lycaenid butterflies, or only woody plants); (ii) samples were not considered representative of the biodiversity of a site (e.g., plot sampled only once in the field season); (iii) if a study counted less than 3 plots. Out of 650 studies reviewed, we retrieved openly available data from 31 studies, constituting the core of our dataset. To maximise the use of existing data around the world and increase statistical power without changing our inclusion standards, we then contacted authors of eligible articles from the 650 consulted studies whose data were not openly available and performed an additional, non-systematic search using Google, Google Scholar and the bibliographies within these scientific articles, always applying the same filtering criteria and data-extraction protocol as for the systematically retrieved studies. All included studies, whether identified through the systematic search or through these complementary routes, were analysed together under an identical hierarchical modelling framework.

Overall, this allowed us to retrieve data for a total of 45 studies and 1682 sites. From each study we recorded: (i) Digital Object Identifier (DOI); (ii) coordinates of each study extent's centroid, either directly from the study, or estimated based on the Method section of each manuscript using Google Maps, and (iii) data on species richness for both plants and butterflies in each of the multiple sites sampled in that study. Spatial data was handled using the World Geodetic System 84 (EPSG: 4326). In some datasets, information on plant and butterfly biodiversity was not directly available (e.g., in appendix or in a repository); in these cases, we capitalized on scatter plots illustrating the relationship between plant and butterfly species richness to extract species richness values using the package “digitizer” (Rohatgi, 2023) in R v 4.2.1 (R Core Team, 2023).

Each study was then characterized in relation to its landscape and regional characteristics. To assess whether landscape-scale disturbance influences the relationship between plants and butterflies, we classified our 45 studies between those that focus on human-dominated (e.g., agriculture fields, cities; $n = 19$) or semi-natural (e.g., forest, grassland, islets; $n = 26$) landscapes.

Additionally, to assess anthropogenic impacts at a broader regional scale, we used the HFI measured in 50-km pixels. The HFI is commonly used to approximate the degree to which human activities influence ecosystems across the Earth. We downloaded HFI at ~1 km resolution for the year 2009 (O. Venter et al., 2016) and, for each study, we calculated the mean HFI value across pixels 50×50 km centred on the centroid of each studied landscape. Note that because information on multiple sampling locations was not available in most studies, we could only retain a single HFI value extracted in the study centroid, in the centre of a 50-km raster pixel, representing the degree to which the landscapes hosting all butterfly and plant communities in that study are influenced by human activities. For a few studies that fell into different

regions (i.e., 50×50 km pixels with different HFI values), we extracted more than one HFI value. However, most studies were located in a single region, and therefore all sites in these landscapes share the same HFI value. This implies that we cannot directly assess the effects of HFI on plant and butterfly diversity, because there is not sufficient replication of communities exposed to different HFIs. The dataset we compiled, nevertheless, allows us to ask questions across all landscapes of how the butterfly ~ plant diversity relationship changes with HFI, which is the objective of our analysis.

Analysis

We fit linear mixed-effect models treating (i) butterfly alpha/beta diversities as response variables; (ii) plant alpha/beta diversities, landscape type, and HFI as fixed effects; and (iii) study identifiers as a random effect.

Alpha diversity was measured as the number of species observed in a sampling site, whereas beta diversity was measured as (gamma-alpha)/gamma, where alpha diversity is the total number of butterfly or plant species at a site, and gamma is the cumulative total number of species in a landscape studied (Anderson et al., 2011). This metric of beta diversity measures the proportion of species missing from a site in comparison to the entire set of species documented in a study, such that high values signify relatively low site-scale (alpha) diversity in comparison to landscape-scale (gamma) diversity. We did not explore other metrics of beta diversity because information on the identity of species across sites was typically not available. Because not all studies reported the total number of species observed across all sites, beta diversity is assessed only for a subset of 24 of the 45 landscapes studied, representing a total of 906 sites.

We used the 'glmmTMB' R package (McGillycuddy et al., 2025) to fit our models, following a frequentist framework for parameter estimation. We included in all models an interaction term between landscape type and plant diversity (alpha or beta), allowing for different slopes and intercepts in semi-natural vs. human-dominated landscape types. We also included an interaction term between regional HFI and plant diversity, allowing the slope of the relationship to vary within the two landscape types. This modelling framework allowed us to estimate whether changes in butterfly biodiversity with plant biodiversity depend on the degree to which landscapes and regions were subject to human activities. We fit random slopes and intercepts at the study level for the effects of plant diversities on butterfly diversities across sites. We standardized HFI values by subtracting the mean and by dividing by the standard deviation. For models of alpha diversity, we log₂-transformed plant and butterfly species richness.

As differences in plot size between studies could influence our inferences, we performed a sensitivity analysis controlling for plot sizes. Because information on exact plot size was not available for all studies and to retain all datasets, we categorized plot sizes into 6 categories: unknown, < 1 ha, 1–10 ha, 10–100 ha, 100–1000 ha, and > 1000 ha. To control for broad differences in sampling extent, we included this predictor as a random effect in the two models.

All data and the script used to run analyses has been uploaded to a Zenodo repository at 10.5281/zenodo.18446361.

Results

Our analysis focuses on changes in alpha and beta diversity from 45 studies where scientists sampled both plants and butterflies across 1682 sites (Fig. 1). On average, sampling sites hosted 12 butterfly species (SD = 10) and 51 plant species (SD = 71), whereas at the study level, approximately 48 butterfly species (SD = 27) and 246 plant species (SD = 150) were recorded (Table 1). Plot size varied among studies from 0.02 to 7853.98 ha, with a median of 1.01 ha for human-dominated landscapes and from 0.01 to 203,400.00 ha and a median at 0.10 ha for semi-natural landscapes.

Human Footprint Index (HFI)

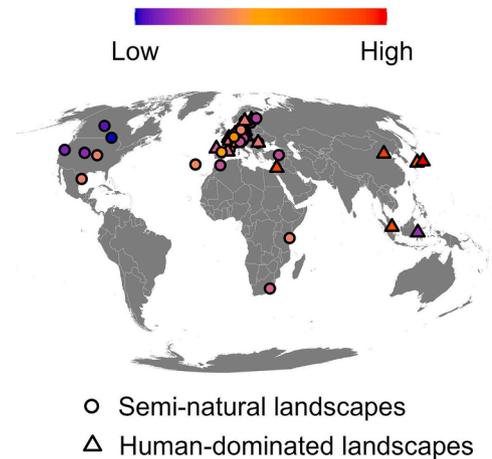


Fig. 1. Map showing the location of the 45 studies synthesized. The shape of the dots represents the landscape type in which each study was conducted, either a semi-natural landscape (circles) or a human-dominated landscape (triangles). The colour gradient represents the standardized Human Footprint Index (HFI) in the region surrounding each study landscape, where blue represents landscapes with little human impact (min HFI = 0.8, scaled value = -1.7), and red represents sites with high human impact (max HFI = 37.9, scaled value = 2.7).

Alpha diversity

For the same number of plant species, our model identified a higher butterfly species richness in (i) semi-natural landscapes, as opposed to human-dominated landscapes, and (ii) in regions with lower HFI (Fig. 2; see Table S1 for model coefficient estimates). While the log₂-transformed number of butterfly species was always positively related to the log₂-transformed number of plant species (coefficient estimate = 0.70, CI = 0.60;0.80, $p < 0.001$), the steepness of this relationship was reduced in human-dominated landscapes (estimate = -0.36, CI = -0.49;-0.23, $p < 0.001$), with support for an interaction between the landscape and regional effects (estimate = -0.04, CI = -0.06;-0.01, $p < 0.01$). This means that less butterflies were found per plant species in disturbed landscapes and regions: for instance, 256 plant species in a site supported ~ 40 and 25 butterfly species in semi-natural vs. human-dominated landscapes at the lowest regional HFI, and these numbers changed to ~ 45 and 12 butterfly species at the highest regional HFI (Fig. 2). While the relationship between plant and butterfly alpha diversity is relatively strong across our studies ($R^2 = 0.31$) and consistent with previous estimates (Castagneyrol & Jactel, 2012; Kral-O'Brien et al., 2021), the standard deviation of the random effect on study ID highlights considerable variation in butterfly species richness across studies (Table S1). The sensitivity analysis showed that results were consistent when controlling for the size of the plot used to assess butterflies and plants within each study (see Tab. S2 and S3). The variance of the random intercept and slope for plot size category was estimated to be zero, indicating that plot size did not explain additional variation in the model.

Beta diversity

When focusing on beta diversity (Fig. 3, Tab. S4), we found the expected positive relationship between butterfly and plant diversities (coefficient estimate = 2.87, CI = 1.93;3.80; $p < 0.001$), and again that anthropogenic disturbance at the landscape (estimate = 0.82, CI = -0.29;1.94, $p = 0.15$) and regional (beta = -0.28, CI = -0.40;-0.16; $p < 0.001$) scales moderate this relationship in interaction (estimate = 0.28, CI = 0.18;0.37, $p < 0.001$). Both relationships have higher

Table 1
Summary of the number of plant and butterfly species and the Human Footprint index across the two studied landscape types. The full dataset is openly available in a Zenodo repository (see Methods section).

| Landscape type | Number of plots | Median Plot size (ha) | Mean HFI (±SD) | Minimum value of HFI | Maximum value of HFI | Mean Number of butterfly species (±SD) | Minimum number of Butterfly species | Maximum number of Butterfly species | Mean Number of plant species (±SD) | Minimum number of plant species | Maximum number of plant species |
|--------------------------|-----------------|-----------------------|----------------|----------------------|----------------------|--|-------------------------------------|-------------------------------------|------------------------------------|---------------------------------|---------------------------------|
| Human-dominated (n = 19) | 610 | 1.10 | 20.32 ± 9.12 | 5.86 | 37.94 | 11.00 ± 10.88 | 0 | 80 | 59.56 ± 84.00 | 2 | 696 |
| Semi-Natural (n = 26) | 1069 | 0.10 | 12.54 ± 6.08 | 0.80 | 33.57 | 12.30 ± 9.43 | 0 | 127 | 46.37 ± 61.12 | 3 | 925 |

uncertainty than in the case of alpha diversity estimates, likely due to the reduced sample size to 24 landscapes.

The model suggests that beta diversity of butterflies (i) tended to be higher in semi-natural landscapes than in human-dominated landscapes (Fig. 3, left vs. right inset) and (ii) decreased with HFI (Fig. 3, blue vs. orange and red lines). For instance, a site containing ~ 10 % of the total plant species in a landscape would host ~ 17 % of butterfly species in human-dominated landscapes, regardless of HFI, and in semi-natural landscapes ~ 9, 21 and 41 % of butterfly species at the minimum, average, and maximum HFI values. In other words, disturbed sites contain a disproportionately high proportion of the butterfly fauna, which is consistent with butterfly assemblages having suffered loss of rare species across all sites in the most disturbed landscapes. Like for alpha diversity, the sensitivity analysis accounting for plot size showed that results were robust to this variable (see Tab S5).

Discussion

Biodiversity knowledge shortfalls limit effective conservation action, but knowledge gaps on biotic interactions (Caron et al., 2024) and cross-scale biodiversity change (Riva & Fahrig, 2023, Riva et al., 2024b) are still widespread. Here we assessed how human activities at the landscape and regional scales impact the relationship between plants and butterflies, two groups tied by obligate biotic interactions (Figs. 2, 3). Based on our results, human activities at both landscape and regional scales affect the relationship between butterfly and plant diversity, with compound effects that are consistent with stronger biotic homogenization of butterfly communities (Anderson et al., 2011).

Interestingly, the effects of regional disturbance, measured with the HFI in 50-km pixels, were detected only in human-dominated landscapes for alpha diversity metrics, and only in semi-natural landscapes for beta diversity metrics. Specifically, our models suggest that: (i) the number of butterfly species found per plant species is lower in human-dominated landscapes than in semi-natural landscapes, and that butterfly biodiversity in a site is further decreased by regional HFI in human-dominated but not semi-natural landscapes (Fig. 2); and (ii) beta diversity of butterflies is lower in human-dominated landscapes than in semi-natural landscapes, and that the negative effect of regional HFI on beta diversity are detectable only in semi-natural landscapes, where homogenization is caused by disturbed regional contexts (Fig. 3). These results might have emerged because of the scales of the two biodiversity metrics. Indeed, alpha diversity is based solely on site-level information, whereas beta diversity includes information about the relationship between local and landscape-scale biodiversity. These results also point at potential negative effects of human activities on two facets of butterfly diversity in relation to plant diversity: loss of species (Fig. 2), and homogenization (Fig. 3). Ultimately, while human-dominated landscapes fare worse than semi-natural landscapes, the negative effects of HFI appear differently between alpha and beta diversity metrics, pointing at complex cross-scale dynamics.

Overall, our findings are consistent with previous empirical evidence that higher trophic levels tend to be more sensitive to the effects of global change (Zavaleta et al., 2009), suggesting that this pattern might extrapolate beyond well-studied vertebrate groups (Henry et al., 2024). More specific to our system, we can speculate as to why butterflies were more sensitive than plants. This could be due to the fact that butterflies have been recognized as an overall sensitive group to anthropogenic stressors (J.A. Thomas, 2016). However, many plant species are also rare and/or sensitive (Enquist et al., 2019). Alternatively, it is possible that the lower number of butterfly than plant species might underlie this result. There are more than 400.000 plant species on Earth (Díaz & Malhi, 2022), whereas only approximately 20.000 butterfly species have been so far described (Pinkert et al., 2022). While in our study we found approximately 5 times more species of plants than butterflies at both the site and study level, biodiversity relationships were affected between the two groups when assessing both alpha and beta diversity, meaning that

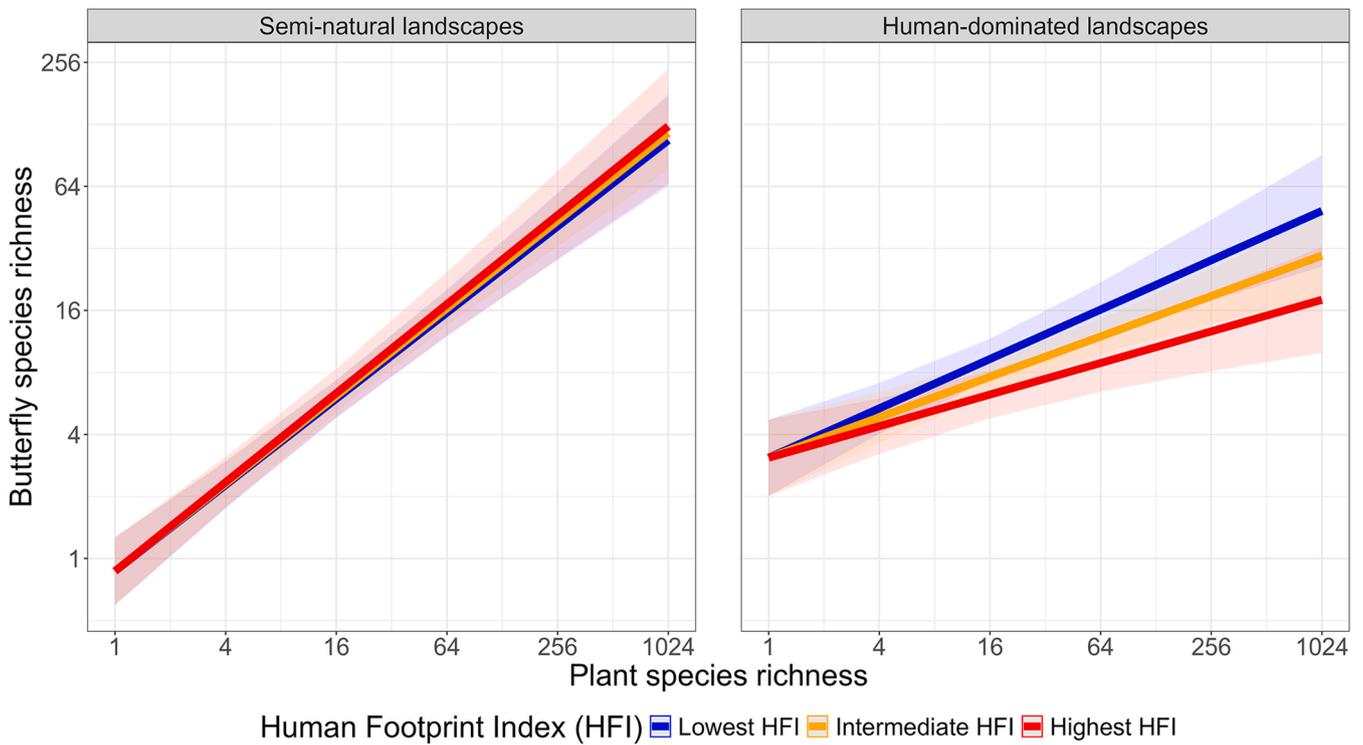


Fig. 2. The relationship between butterfly and plant species richness responds to human activities at the landscape and regional scales. At the landscape scale, semi-natural landscapes (left inset) have generally higher butterfly diversity than human-dominated landscapes (right inset) for the same total number of plants. At the regional scale, landscapes surrounded by higher HFI show further depressed butterfly species richness for the same plant richness, but only in human-dominated landscapes (right inset).

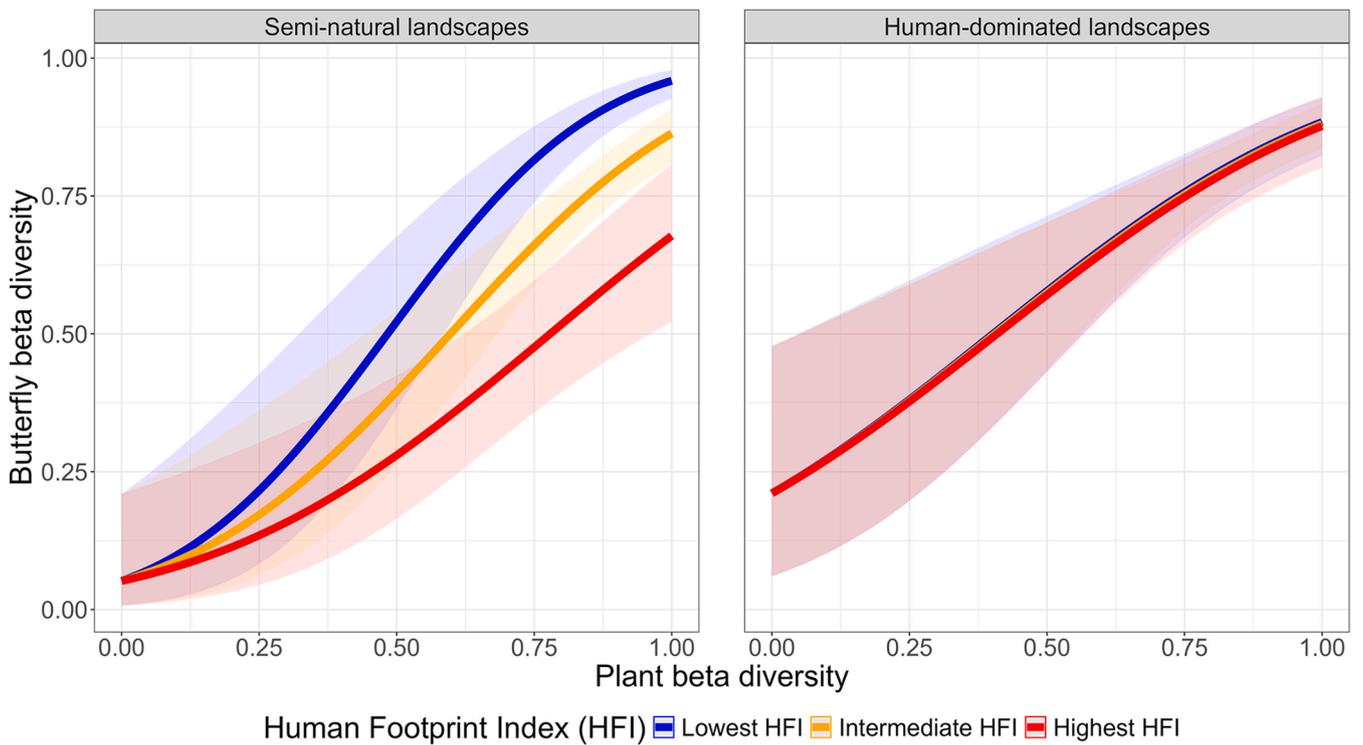


Fig. 3. The relationship between butterfly and plant beta diversity (proportion of species missing from a site in comparison to the entire set of species documented in a study) responds to human activities at the landscape and regional scales. At the landscape scale, semi-natural landscapes (left inset) have higher butterfly beta diversity than human-dominated landscapes (right inset) for the same plant beta diversity. At the regional scale, landscapes surrounded by lower regional HFI showed increased beta diversity, but only for semi-natural landscapes. This suggests that butterfly assemblages in human-dominated landscapes, or in semi-natural landscapes surrounded by regions with high HFI, have experienced biotic homogenization.

the effects were not restricted to the total diversity in a site, but also to the relationship between local and landscape-scale assemblages.

Trends in feeding strategies across butterfly species might help contextualizing our results. While some butterfly species are generalist and can feed on several plant taxa during their larval stage (Narango et al., 2020), many rely on a limited range of plant taxa for their larval development (Shirey et al., 2022), with most species of butterflies being hypothesized to feed on a single family of larval host plants (Kawahara et al., 2023). This relatively specialized diet strategy suggests that the capacity of plant communities to buffer losses in species richness might be higher than that of butterfly communities, because for the many butterfly species that are either monophagous or oligophagous during the larval stage. In other words, it is likely that a loss of larval host plants at a site due to anthropogenic stressors will result in local extinctions for a butterfly species (Pearse & Altermatt, 2013). More detailed data (e.g., information on species identities and traits) is needed to test different mechanisms potentially underlying the emergent pattern we observed.

Overall, our results are consistent with mounting empirical evidence that human activities are altering long-standing, macroecological relationships between the biodiversity of taxa linked by trophic interactions. We note that this has been identified as a major risk factor for global biodiversity conservation in vertebrates (Fricke et al., 2022), but remains poorly understood for plant-invertebrate relationships.

Implications for conservation

Based on the results of our analyses, we provide three insights for applied biodiversity conservation.

First, our results suggest that “secondary” or “cascading” extinctions are not commonly avoided by butterflies inhabiting anthropogenic landscapes via buffering mechanisms (Brodie et al., 2014; Colwell et al., 2012). Previous studies have shown that some butterfly species are capable of shifting to a different larval host plant to avoid extinction (Singer & Parmesan, 2021), however our results suggest that similar adaptive mechanisms might be uncommon. Conservation scientists and managers should therefore not rely on the hope that butterflies at risk of losing larval host plants – either because of land use or climate change – will be able to adapt and shift to a different host. Such shifts might happen, but rarely and presumably at temporal scales longer in comparison to the current tempo of global change (Allio et al., 2021). When considering that climate change will differentially affect plant and butterfly species, increasing vulnerability of butterflies adapted to sensitive environments (Filazzola et al., 2020), and that insects being already neglected in conservation (Chowdhury et al., 2023), our studies suggests that we should urgently understand how butterfly conservation action can be optimized to include more explicitly information on plant communities.

Second, our findings suggests that large-scale patterns of human activities can mediate local responses to land use change (Riva et al., 2023), and implies that conservation actions targeting only local site conditions are likely to miss important aspects related to regional conditions (Harrison & Cornell, 2008; Ricklefs, 1987; Riva et al., 2023).

Last, the fact that the relationships between both alpha and beta diversities of butterflies and plants respond to landscape- and regional-scale disturbances questions the robustness of studies that use butterfly species richness as an indicator of plant species richness across sites that vary in terms of anthropogenic disturbance. While the two groups are strongly related (Castagneyrol and Jactel, 2012), our results highlight that such relationships change depending on the degree to which human activities have already occurred in a given region. This fact might explain why some studies have found butterflies to be poor indicators of plant diversity [e.g., in logged forests across Madagascar; (Kremen, 1992)], whereas other found the opposite [e.g., montane forests within a park in Colorado (Simonson et al., 2001)].

Limitations

Before concluding, we acknowledge some limitations of our study. For instance, we did not differentiate between native vs. non-native species of plants; however, given the diversity of species in our samples, we expect the effects of introduced species to be minimal given that typical biodiversity datasets count < 5 for such species (Liu et al., 2023). Our analysis is also based on a biased sample of the planet, with limited data from the tropics and no data from traditionally underrepresented regions. Most landscapes analyzed are located in Europe ($n = 27$), whereas Africa, Oceania, and South America are severely underrepresented ($n = 7$) (Fig. 1). We searched for studies in these regions with a non-systematic literature review, but failed to find available datasets.

Conclusions

We showed that human activities at landscape and regional scales alter relationships between the biodiversity of plants and butterflies, with butterflies being more sensitive to anthropogenic disturbance than plants. Relationships between alpha and beta diversities of butterflies and plants are comparatively strong, reflecting the signature of millions of years of coevolution between these two groups, yet they are not immune to the effects of anthropogenic disturbance. That effects of landscape types and regional HFI were detected even when assessing these very general, emergent patterns of association between the two taxa (Figs. 2, 3) suggests that the plant-butterfly system is a promising system to study the ecology and conservation of obligate interactions in more detail. Follow-up studies assessing species identities and traits will allow better discriminating the mechanisms underlying why such relationships changed with anthropogenic disturbance.

More broadly, our study hints at subtle ways in which human activities are affecting ecosystems globally. Effects on the biodiversity relationships would not be possible to detect when focusing on either plants or butterflies alone, and have not (to our knowledge) previously documented at these scales of analysis. Nevertheless, the most common approach in conservation continues to be a focus on specific taxa, independently from their interaction (Heinen et al., 2020), and on arbitrary scales. As anthropogenic disturbances are expected to increase globally (J.A. Venter et al., 2016), effects like the one we documented will become more widespread, potentially jeopardizing the stability of ecosystems (Hooper et al., 2012). We hope that this analysis will be one of many recent calls for the scientific community to think about the potential implications of global change on biotic interactions.

Data availability statement

The data is available on Zenodo at <https://zenodo.org/records/18446361>.

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CRediT authorship contribution statement

Miguel Cruz Palma: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Antoine Guisan:** Writing – review & editing, Conceptualization. **Shawan Chowdhury:** Writing – review & editing, Conceptualization. **Flavien Collart:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis, Conceptualization, Data curation. **Federico Riva:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baec.2026.02.002](https://doi.org/10.1016/j.baec.2026.02.002).

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