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**Human activities alter the relationship between plant  
and butterfly species richness.**

**Travail de Maîtrise universitaire ès Sciences en comportement, évolution et  
conservation**

*Master Thesis of Science in Behaviour, Evolution and Conservation*

par

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## Abstract

Plants and butterflies share an intricate relationship, involving many interactions such as herbivory pressure and pollination. Understanding how this relationship changes is important to conduct effective and rapid biodiversity conservation measures, because we are experiencing a global biodiversity crisis. In this study, we aimed to understand how the relationship between the diversity of plants and butterflies changes through human activity. To this end, we combined a cross-taxon correlation approach with an ecological review. By assessing 56 relationships between butterfly species richness and plant species richness, extracted from 56 studies and representing more than 1900 sites, we found that butterfly species richness manifests a greater sensitivity to human impact. This result reflects the known sensitivity of the butterfly taxon along human impacted gradients and hints at an overall decline trend for this charismatic group, leading to a potential reduction in the ecosystem services provided by butterflies in areas of human importance. More specifically, the Europe and Asia regions present higher human impacted values. We suggest the application of in-depth butterfly conservation measures in these regions, such as the enrichment of native plant species and the eradication of alien ones, which would ultimately highlight the plant-pollinator relationship on a global scale.

**Keywords:** butterflies, plants, human impact, cross-taxon correlation, biodiversity conservation.

## Résumé

La relation entre les plantes et les papillons est complexe, impliquant de nombreuses interactions telles que la pression herbivore et la pollinisation. En raison de la perte de biodiversité à l'échelle mondiale, la compréhension des changements opérant dans cette relation est nécessaire pour établir des mesures de conservation rapides et appropriées. Dans cette étude, nous avons cherché à comprendre comment cette relation réagit face à l'impact des activités humaines. Pour ce faire, nous avons opté pour une méthode utilisant l'approche inter-taxons avec une revue systématique. Grâce à cette méthode, nous avons réussi à obtenir un jeu de données comprenant jusqu'à 56 études, couvrant la biodiversité des plantes et des papillons pour plus de 1900 sites différents. Notre étude montre que la biodiversité des papillons manifeste une plus grande sensibilité à l'impact humain, comme le relève l'analyse des 56 relations entre la richesse des plantes et des papillons. Ce résultat reflète la sensibilité déjà

étudiée du taxon des papillons le long des gradients impactés par l'activité humaine et indique un déclin général pour ce groupe charismatique, conduisant à une réduction potentielle des services écosystémiques fournies par les papillons dans les zones d'intérêt humaines. Plus précisément, les régions d'Europe et d'Asie présentent des valeurs d'impact humain élevées. Ainsi, nous suggérons l'application de mesures appropriées de conservation pour les papillons dans ces régions, telles que l'éradication des espèces végétales exotiques par leur remplacement d'espèces végétales indigènes, mettant en évidence l'importance de la relation entre plantes et pollinisateurs à l'échelle mondiale.

## Introduction

The current loss of biodiversity concerns both species and the integrity and functionality of ecosystems and has reached an all-time crisis point, resulting in an extinction rate up to 100-1000 times higher than natural extinction rates (Braje & Erlandson, 2013; Cowie et al., 2022; Marcus, 2018). Through phenomena such as overexploitation, habitat loss, introduction of alien species and climate change, current species extinction is quantitatively and qualitatively distinct from the past mass extinctions. Current species decline is different as species extinct are "without replacement", marking no evolutionary species change over a longer-term evolutionary period. This phenomenon is already resulting in changes in phylogenetic diversity and spatial patterns attributed to anthropogenic pressures (Ceballos et al., 2015; Marcus, 2018). Consequently, human pressures are driving biodiversity rapidly towards the sixth mass extinction (Cowie et al., 2022).

Ecosystems typically involve herbivores feeding on plants, which, in turn, become the prey of predators. This relationship illustrates the dependencies among plants, herbivores and predators for their survival (Castagneyrol & Jactel, 2012). Due to these intricate dependencies, it was hypothesised and further demonstrated that an increase in plant diversity positively increases animal diversity (Castagneyrol & Jactel, 2012; Lewinsohn & Roslin, 2008). This is attributable to the low trophic position of plants, which supports the diversity of herbivores and, consequently, their predators (Holmes & Blubaugh, 2023). Castagneyrol and Jactel (2012) conducted a comprehensive analysis of a dataset including over 300 case studies, demonstrating the generality of the cross-taxa correlates between plant and animal species richness across large trophic levels, spatial extents and habitats.

Numerous relationships between plants and animals have been documented (Castagneyrol & Jactel, 2012). Among them, pollination - the mutually beneficial interaction between flowering plants and animals in an ecological context - is interesting to study cross-correlation correlates (Lunau, 2004; Waser & Ollerton, 2006). Flowering plants constitute the most diverse group of land plants (Christenhusz & Byng, 2016) and receive pollination from a diverse array of pollinators, from vertebrate animals, like birds and bats, to insects, particularly those belonging to these four orders: Coleoptera, Diptera, Hymenoptera and Lepidoptera (Waser & Ollerton, 2006).

The relationship between plants and pollinators is mutualistic in many regards. Pollination ensures sexual reproduction in flowering plants by dispersing pollen and maximising its dispersal range through the development of fruit ripening (Buchmann & Nabhan, 2012; Gabriel & Tschardt, 2007). Meanwhile, pollinators benefit from flowers providing food essentials (nectar or pollen) or chemical compounds used for protection against predators or for reproductive traits to attract mates (Kiestler et al., 1984; Waser & Ollerton, 2006). Varying degrees of specialisation exist within this mutualistic relationship, resulting from distinct evolutionary processes (Lunau, 2004; Morgan, 2000). While the mutualistic association between plants and pollinators spans a broad scope, from non-specific interactions to hyper-specific interactions engaging pollinator species with a particular plant species. The strength of this relationship puts 90% of flowering plants in partial or complete reliance on pollinators to maintain the genetic variability and diversity of flowering plants (Kearns & Inouye, 1997; Kiestler et al., 1984; Waser & Ollerton, 2006).

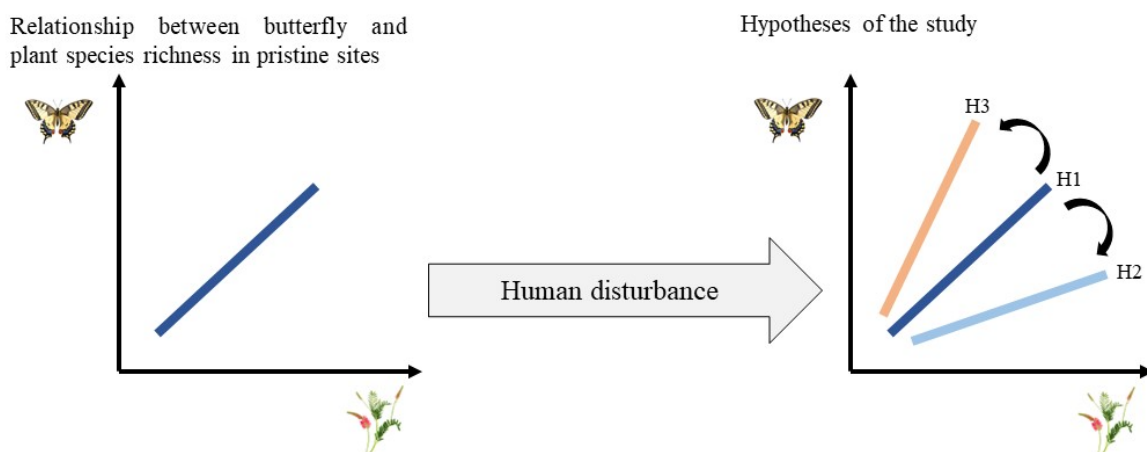
Butterflies (Lepidoptera: Papilionoidea) are a highly charismatic group of pollinators, widely recognised and appreciated for their diverse ecological roles, cultural value, and beauty (Pe'er & Settele, 2008; Rahman et al., 2018). Butterflies undergo metamorphosis (Cinici, 2013) through a holometabolous cycle (Legal, 2022), divided into two phases: the immature and mature stages (Radchuk et al., 2013). The immature stages include eggs (static state), caterpillars or larvae (mobile state and herbivorous stage), and pupae or chrysalides (static state). Finally, the mature stage solely includes the adult butterflies, also called "imagines" (dispersal state and reproductive stage) (Cinici, 2013; Legal, 2022). The entire life cycle of butterflies is closely interconnected to the presence of plants. Winged adult butterflies require host plants (which can include all clades of land plants but predominantly flowering plants) to lay either their single or cluster eggs (Levin, 2001). As soon as they hatch, caterpillars start an

herbivorous diet, feeding on leaves and other vegetative parts. Once their growth is achieved, caterpillars cease to feed on the host plant and look for a suitable location to pupate (chrysalis) (Babošová et al., 2021; Cinici, 2013; Levin, 2001). Finally, when metamorphosis is complete with fully expanded and dried wings, adult butterflies transition to feeding on floral resources, specifically pollen and nectar, characterizing butterflies as effective pollinators (Boggs et al., 2003).

For the reasons described above, the relationship between plant and butterfly biodiversity is strong (Ehrlich & Raven, 1964). Concurrently, this relationship is not symmetrical (Narango et al., 2020). This is because a restricted number of plant species support a larger proportion of Lepidoptera species. These restricted plant genera, named "keystone plant genera" are considered as a small hyper-productive group for maintaining Lepidoptera's caterpillars and comprise merely a fraction of the native flora (Narango et al., 2020).

As we have entered the Anthropocene, it is important to understand the asymmetries in the relationship between plants and butterflies to address their weaknesses as effectively as possible. Increasing human population and the expansion of built-up areas might lead to poor habitat quality for plants and butterflies (Kuussaari et al., 2021; Piano et al., 2020; Williams et al., 2015), and this spatial restriction engenders severe reductions in butterflies and native plant species richness (Kuussaari et al., 2021). Being a particularly highly sensitive taxon, butterflies show increased sensitivity to urbanisation, recording severe declines along the rural-urban gradient (Sing et al., 2016). Factors such as short life cycles and subtle ecological requirements contribute to poor adaptability in urban environments (Kuussaari et al., 2021; Saadat et al., n.d.). Specifically, butterfly species richness is influenced by local habitat quality (Aguilera et al., 2019; Kuussaari et al., 2021) and connectivity (Kuussaari et al., 2021; Lizée et al., 2012), linked to species-specific traits, from habitat specificity to mobility and voltinism (Kuussaari et al., 2021). While butterflies are highly impacted in anthropogenic environments, plant species richness can be richer, e.g., when favoured by human management practices (such as agroforestry) and with the introduction of alien species (Öckinger et al., 2009; Sing et al., 2016). Along with ruderal species, alien plant species thrive in urban areas, analogous to the success of highly mobile and pioneer plant species (Concepción et al., 2015; Lososová et al., 2012; Sing et al., 2016). Whether the plant species suffering from human land use are "keystone larval host plants", however it is unknown.

In this context, we aimed to investigate how the relationship between plant and butterfly species richness varies across the degree of human activities. Considering the mutualistic and asymmetric relationship between plants and butterflies, and the different potential responses in these taxa to human activities, we developed three hypotheses concerning the human impact on the relationship between plants and butterflies. The first hypothesis (H1) postulates human impact would have similar repercussions for both butterfly and plant species richness, leading to an unaffected linear relationship in highly-modified landscapes (Fig. 1). In this case, even if human impact led to a significant reduction in both plant and butterfly species, their linear relationship would remain unchanged compared to pristine sites, suggesting similar responses between the two groups. The second hypothesis (H2) posits a greater decline in butterfly species richness, resulting in shallower slope of their correlation compared to a pristine environment. In this case, human pressures would affect stronger butterfly species richness and/or mark an increase in plant species (e.g., due to the addition of invasive species) (Fig. 1). Finally, the third hypothesis (H3) posits that human impact might disproportionately deplete plant diversity. This hypothesis could be, e.g., the result of rarer plant species extinction. In this scenario, a sharper decrease in plant species richness compared to butterfly species richness would result in a steeper linear relationship compared with a pristine environment (Fig. 1). This is because, typically, there are many more plant species than butterfly species in a site, and thus differential extinction of rare species might comparatively affect more plant species than butterfly species.



**Figure 1. Relationship between plant and butterfly species richness, and its potential change with human disturbance in light of three key hypotheses.** Hypothesis 1 (H1) posits resilience to disturbance, pointing up the interdependence between butterfly and plant species richness. Hypothesis 2 (H2) suggests a reduction in butterfly diversity. Hypothesis 3 (H3) illustrates a relative decrease in plant diversity.

# Methods

Following guidelines for systematic reviews in ecology and conservation biology (Foo et al., 2021; Grames & Elphick, 2020; Pullin & Stewart, 2006), we designed a literature review aimed at investigating a specific goal: understanding the variation in the relationship between plant and butterfly species richness across a degree of intensity in human activities. Specifically, we investigated the impact of human activities on the relationship alpha diversity (i.e., species richness, or number of species) of these groups (Thukral, 2017) across multiple sampled sites in each of many studies. Therefore, (i) we set up a methodological workflow to find studies with sampling data on plant and butterfly species richness at multiple sites. We assessed (ii) how each study area is affected by human activities using the human footprint (Venter et al., 2016, 2018). Finally, (iii) we modelled the relationship between butterfly richness (dependent variable) and plant richness (independent variable), including human footprint and as model covariate (fixed effect) while controlling for study landscape (random effect; see below the model formula).

## Data gathering for plant and butterfly richness.

We used The "Web Of Science Core Collection" (WoS; <https://www.webofscience.com/wos/woscc/basic-search>) platform to gather studies (and thus data) on plant and butterfly richness (Calver et al., 2017). This database allowed us to encompass the world's leading scholarly journals, books and proceedings in sciences from 1900 to the date of the research, May 12, 2023. To achieve a recommended high sensitivity and relatively low specificity string research (Nielsen et al., 2014; Pullin & Stewart, 2006), we ended up with the following formula:

```
(ALL=(butterfl*) OR ALL =(Rhopalocera)) AND (ALL=(plant*) OR ALL = (angiosperm*))  
AND (ALL=(species richness) OR ALL = (biodiversity))
```

We collected a total of 1714 papers from the research in WoS, resulting in a downloaded table including essential details such as the DOI links, author names, articles, and source titles (see Table S1). We added two columns to assign a unique identifier to each paper (1 to 1714) and indicate each article's relevance to our study. To avoid bias in the order of appearance of papers, we randomized the order of the scientific papers and then checked the first 650 papers.

After the gathering stage, the data extraction and assessment followed as the second stage. We established inclusion and exclusion criteria for the evaluation of papers relevant to our study design (Grames & Elphick, 2020; Pullin & Stewart, 2006). In this regard, we did not record studies (i) if the diversity of plant and butterfly species was limited to a subset of species (e.g., only a few indicator species assessed), or (ii) if they were based on samples not representative of the biodiversity of a site (e.g., relationship between plant and butterfly diversity based on a single sample in one year). We retained only studies where a study area was assessed or characterized with exhaustive surveys of multiple sites ( $\geq 3$  plots; mean = 18.4; SD = 11.9), with species richness of vascular plants (or, at the very least, flowering plant) and of butterflies.

Extracting data from the literature using the WoS table demonstrated challenging. The string search resulted in several papers not appropriate for our goal. For instance, we found exclusively butterfly richness or plant richness, leaving one of our groups of interest unsampled. In cases where both richness of plant and butterfly richness were sampled, one of the sampled groups of butterfly and plant (or both) didn't meet the criteria of our analysis study (e.g. one butterfly species sampled, only tree plants sampled, etc.). Last, we did not consistently met the minimum requirement of three sampling sites, or "sampling sites" were characterised in some studies as a type of landscape encompassing multiple sampling locations that were not available to the public (e.g., the average richness for 10 forests contrasted to the average richness for 10 cities).

Due to these challenges, we utilized additional sources, such as Google Scholar (<https://scholar.google.com/>). If we found a study outside the WoS table and further added to our dataset, its appearance was checked on the rest of the WoS table and marked if it was present. Out of 650 studies found and assessed in and outside the WoS table, we retained a total of 56 studies for our dataset (Table 1). We directly retrieved openly available data (Table 1) from 31 studies within and outside the WoS list. Furthermore, when scatterplots depicting the linear relationship between plant and butterfly species richness were present, we performed data scraping to extract species richness values using the package "digitizeR" in R v4.2.1 (R Core Team 2023), contributing to 14 datasets (Table 1). Moreover, we contacted the authors of articles identified as containing butterfly and plant species richness in multiple sites, but which data was not openly available. Through this process, we added 13 papers out of the 56 collected; an additional 78 e-mails went unanswered or yielded unusable data for our analysis (Table 1).



**Table 1. Assessment of papers for extracting butterfly and plant surveyed richness data.**

The table is presented in ten rows, displaying (i) papers retained for the study from the first 650 assessed articles on the Web Of Science (WoS) list, (ii) the complete list of papers retained from the WoS list, including papers beyond the 650th assessed that were added using a more specific search on Google Scholar, (iii) papers retained outside the WoS list, and finally, (iv) the number of unfruitful e-mails sent during the data collection process (see Table S1).

Papers	Papers' ID in our study	Identifier number from the WoS table	Total number of papers
Papers found in WoS table: checked up to 650 <sup>th</sup> paper	2, 3, 4, 5, 6, 9, 10, 11, 13, 14, 15, 17, 18, 19, 20, 21, 23, 24, 25, 27, 28, 30, 31, 33, 35, 36, 39, 40, 43, 53, 54, 56	5, 17, 25, 31, 84, 509, 107, 148, 580, 241, 326, 589, 336, 393, 470, 606, 363, 626, 461, 640, 650, 612, 624, 632, 593, 576, 425, 14, 294, 290, 266, 620	32
Papers selected from the entire WoS table	1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33, 35, 36, 39, 40, 41, 42, 43, 46, 47, 49, 50, 51, 53, 54, 56	1553, 5, 17, 25, 31, 84, 1527, 509, 107, 148, 1133, 580, 241, 326, 1106, 589, 336, 393, 470, 606, 363, 626, 461, 1443, 640, 650, 1035, 612, 624, 632, 593, 576, 425, 14, 899, 1446, 294, 1676, 1335, 1663, 1480, 1152, 290, 266, 620	45
Papers retained in the study but absent from the WoS list	7, 22, 32, 34, 37, 38, 44, 45, 48, 52, 55	\	11

Papers in the WoS table where authors shared data	11, 15, 18, 23, 24, 27, 30, 39, 49, 54, 56	148, 326, 336, 363, 626, 640, 612, 425, 1663, 266, 620	11
Papers absent from the WoS table where authors shared data	32, 44	\	2
Papers in the WoS table with data collected through scraping	12, 13, 16, 17, 26, 35, 41, 46, 47, 50, 53	1133, 580, 1106, 589, 1443, 593, 899, 1676, 1335, 1480, 290	11
Papers absent from the WoS table with data collected through scraping	7, 38, 48	\	3
Papers in the WoS table with data present in the published version	1, 2, 3, 4, 5, 6, 8, 9, 10, 14, 19, 20, 21, 25, 28, 29, 31, 33, 35, 36, 40, 41, 42, 43, 51	1553, 5, 17, 25, 31, 84, 1527, 509, 107, 241, 393, 470, 606, 461, 650, 1035, 624, 632, 593, 576, 14, 899, 1446, 294, 1152	25
Papers absent from the WoS table with data present in the published version	22, 34, 37, 45, 52, 55	\	6
Papers in the WoS table for which emails requesting data resulted in unanswered or unshared data by authors	\	51, 92, 96, 110, 167, 173, 180, 196, 207, 212, 215, 221, 252, 260, 273, 276, 280, 284, 305, 319, 339, 350, 363, 373, 390, 392, 400, 402, 406, 412, 415, 426, 433, 440, 457, 463, 464,	78

		466, 467, 478, 479, 483, 505, 512, 513, 517, 526, 527, 532, 537, 544, 545, 550, 559, 561, 563, 656, 567, 575, 584, 590, 594, 598, 601, 604, 607, 611, 614, 615, 621, 631, 636, 645, 647, 1037, 1254, 1332, 1689	
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### Creation of dataset for analysis

For each study, we recorded various types of information. We stored the DOI link assigned to each study for ease of consultation and assigned a numerical identifier based on its inclusion order in the dataset. We reported data on species richness for both plants and butterflies. Additionally, we recorded the corresponding type of plant samples; not all studies recorded all vascular plant species, and we controlled for this variation across studies in our model. Depending on the characteristics of the sites studied, we assigned one of six different landscape types that are known to influence the number of butterflies and plants: native (i.e., the study was conducted primarily in native vegetation, such as pristine forests or grasslands), islands, grasslands, forests, agriculture and urban landscapes. When assigning these categories, we reasoned that human activities would have a stronger impact on the relationship, and thus prioritize those in limit cases. For example, if the site or the entire study exclusively comprised sites within a grassland environment, but such grasslands were embedded in an urban environment strongly influenced by human activities, then we kept the “urban” category over the “grassland” classification. Regarding the “islands” category, we considered studies or sites as such when they represented small islands in freshwater environments (e.g., the lake islands in Sabaskong Bay, Canada) or marine environments (e.g., the Azores islands), as long as the entire island was considered as a single survey site. As a result, we excluded large islands such as the main island of Singapore (Pulau Ujong) or the Japanese Archipelago from the island category, and treated instead as any other terrestrial site. Most sites in the dataset corresponded

to grassland landscape (931), followed by agriculture (387), urban (323), forest (212), island (79) and native (23). In order to contrast between pristine and urban landscapes, and because differences between non-disturbed landscapes were minimal, we ended up considering forest, grassland, and island landscapes as ‘native’, leading up to 1245 sites classified as native, 387 as agriculture and 323 as urban, with a total of 1955 observations in the dataset.

We obtained the coordinates of each study extent's centroid either directly from the study, or estimated them using Google Maps (<https://www.google.com/maps>). We noted all centroid coordinates per study under the WSG84 system (World Geodetic System 1984). If coordinates were recorded for each sampling site, then we calculated the mean to obtain a single centroid coordinate when plotting a global map representing the geography of our samples. We needed to collect a single centroid coordinate per study to further extract the according Human Footprint Index and Biome values on this exact coordinate in R v 4.2.1 (R Core Team, 2023). We selected the Human Footprint Index (HFI) to measure the human impact in our study areas, given its utility for biodiversity conservation purposes (Keys et al., 2021; Venter et al., 2016, 2018). The HFI aids in determining the state of biodiversity in the face of land use changes and supports the formulation of policies regarding human pressure impact (Beyer et al., 2020; Keys et al., 2021). Several advantages are highlighted: providing a global map, this tool is a dimensionless metric capturing the extent of human impact on the diverse terrestrial biomes (Keys et al., 2021; Venter et al., 2016, 2018). To calculate the HFI, eight different factors were synthesized, including built-up environments, population density, electric power infrastructure, crop lands, pasture lands, roads, railways and navigable waterways. We downloaded the HFI data at ~1 km resolution for the year 2009 (latest version available) from the dataset offered by the Socioeconomic Data and Applications Center (SEDAC) (<https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-2009-human-footprint>; (Venter et al., 2016, 2018)). We extracted biome and HFI data using the terra package (Hijmans et al., 2023). For HFI, we extracted the mean value across a pixel of 50\*50km centred to each study centroid which ensured the cover of the entire study area.

## **Data analysis**

We conducted all analyses, including the multilevel mixed-effect model, on R v 4.2.1 (R Core Team, 2023). Prior to the statistical analyses, we transformed three variables to enhance the performance and interpretability of a model (Harrison et al., 2018; Hijmans et al., 2023). We started by log<sub>e</sub>-transforming both species richness of butterflies and plants due to the wide

variation obtained on the relative scale of our data, ranging from 1 to 128 for butterflies per site and from 1 to 4138 for plants per site. In order to make the model more additive, the log<sub>2</sub>-transforming reduces the variation between species richness values, rendering the values more linear and easier to interpret (Packard, 2014). The second variable we transformed was the human impact (Mean\_HFI), which represents the second fixed-effect predictor of butterfly species richness (Log2Butterfly) along with plant species richness (Log2Plant). By using the function `scale()`, each value of the continuous variable was centred, subtracted by the mean of the variable and finally divided by the standard deviation of the variable. Standardisation results in a mean of zero and a standard deviation of 1 (Harrison et al., 2018). The purpose of standardization is to facilitate convergence of the model for easier interpretation of the main effects, precisely when the model includes interactions between variables, such as between plant species richness (Log2Plant) and human impact (Mean\_HFI) as in our model (Harrison et al., 2018; Schielzeth et al., 2020). Scaling our HFI contributes therefore to the model stability, the likelihood of model convergence and the accuracy of parameter estimates (Harrison et al., 2018).

For the dataset analysis, we chose a linear mixed-effect model (Harrison et al., 2018; Schielzeth et al., 2020). Linear mixed-effect models incorporate both fixed and random effects (Bolker et al., 2009; Harrison et al., 2018), with the choice of both effects playing a key role in model fit (Harrison et al., 2018). Fixed effects allow for the inclusion of variables of primary interest and enable the fundamental research question to be addressed (here, the potential human impact on the relationship between plant species richness and butterfly species richness). Although at times not considered to be of primary interest, random effects can enhance the interpretability in the establishment of a complex model. Random effects can account for similarity in a number of observations belonging to a specific group within the dataset (non-independent observation units), e.g. species richness might be more similar in the own study in comparison to the other studies of the data and species richness might be more similar in its own landscape in comparison to the other landscapes (Harrison et al., 2018). Specifically, we fitted the mixed-effect model into a multilevel context to incorporate dependency structures in the data that might affect our inference (i.e., the three landscape types in the habitat variable, and the fifty-six different studies in the study.ID variable) (Bürkner, 2017). The biome variable was excluded from the final model after confirming that it did not influence our results. In order to run this mixed effect model in R, we used the 'brms' package (Bürkner, 2017). The brms package allows fitting models using Bayesian inference through the Stan language (Bürkner, 2017).

Bayesian inference is a growing approach in ecology, particularly in studies of population dynamics and ecosystem processes (Ellison, 2004). Bayesian statistics arise from Bayes' theorem, which is applied to characterize a quantitative model based on the dataset under study. In other words, the data is used to generate a posterior distribution in conjunction with a prior probability distribution representing our understanding of the system before the analysis (Bolker et al., 2009; Ellison, 2004; Van De Schoot et al., 2021). We here used uninformative priors. The resulting posterior distribution serves to infer which hypotheses had the highest support (Van De Schoot et al., 2021) (Fig. 1). In contrast to classical frequentist statistics, Bayesian statistics display an alternative perspective to represent the degree of belief in ecological models and a quantitative measure of the probability of a hypothesis being true. More specifically, Bayesian inference defines probability as an individual's degree of belief in the likelihood of an event. This approach therefore provides a measure of uncertainty for the various parameters within models (Ellison, 2004). However, the parameter estimates of the same mixed effect model are virtually identical when fitting the model in either a traditional frequentist approach, or with a Bayesian approach.

Our multilevel mixed-effect Bayesian model (fit1) assesses the relationship between butterfly species richness and the combined fixed and random effects. Butterfly species richness forms the response part of the formula ( $n = 1955$  observations, with each observation being a site from 56 studies and 3 habitat types), which is on the left-hand side of the tilde sign ( $\sim$ ) in R notation, while the random and fixed effects are on the right-hand side as part of the predictor variables. We included in the model an interaction term between plant species richness (Log2Plant) and human impact (Mean\_HFI). This interaction term allows the model to estimate whether changes in butterfly richness with plant richness depend on the HFI. For random effects, we chose one group-level term - plant species richness - as the only coefficients ( $1 + \text{Log2Plant}$ ) varying with the group factors study.ID ( $1 + \text{Log2Plant} | \text{study.ID}$ ) and habitat ( $1 + \text{Log2Plant} | \text{habitat}$ ). This formulation allows the effects of plant diversity to vary with HFI, recognizing that there will be more similar trends within habitats of the same type, and within data points in the same study (crossed random effect). The model formula coded in R is:

```
fit1 <- brm(formula = Log2Butt ~ Log2Plant * Mean_Hfi + (1+Log2Plant|study.ID) +  
(1+Log2Plant|habitat),  
           data = data,  
           seed = 123,  
           chains = 4,  
           cores = 10)
```

We assumed a linear Gaussian model (normal distribution of observed values of butterfly richness around the predicted relationship) (Bürkner, 2017, 2018; S, 2010). Our Bayesian model employs the Markov Chain Monte Carlo (MCMC) algorithm to draw random samples from the posterior distribution. This algorithm is essential to obtain accurate estimates of uncertainty by using different chains simultaneously to converge. Convergence of MCMC was assessed by evaluating the Rhat statistic, which is based on comparison between the estimates for model parameters in the chain itself and between the chains. We run the model with the default number of MCMC (4), each characterised by 2000 iterations with a warm-up period of 1000 iterations (to calibrate the posterior sampling procedure), giving a total of 4000 post-warmup draws.

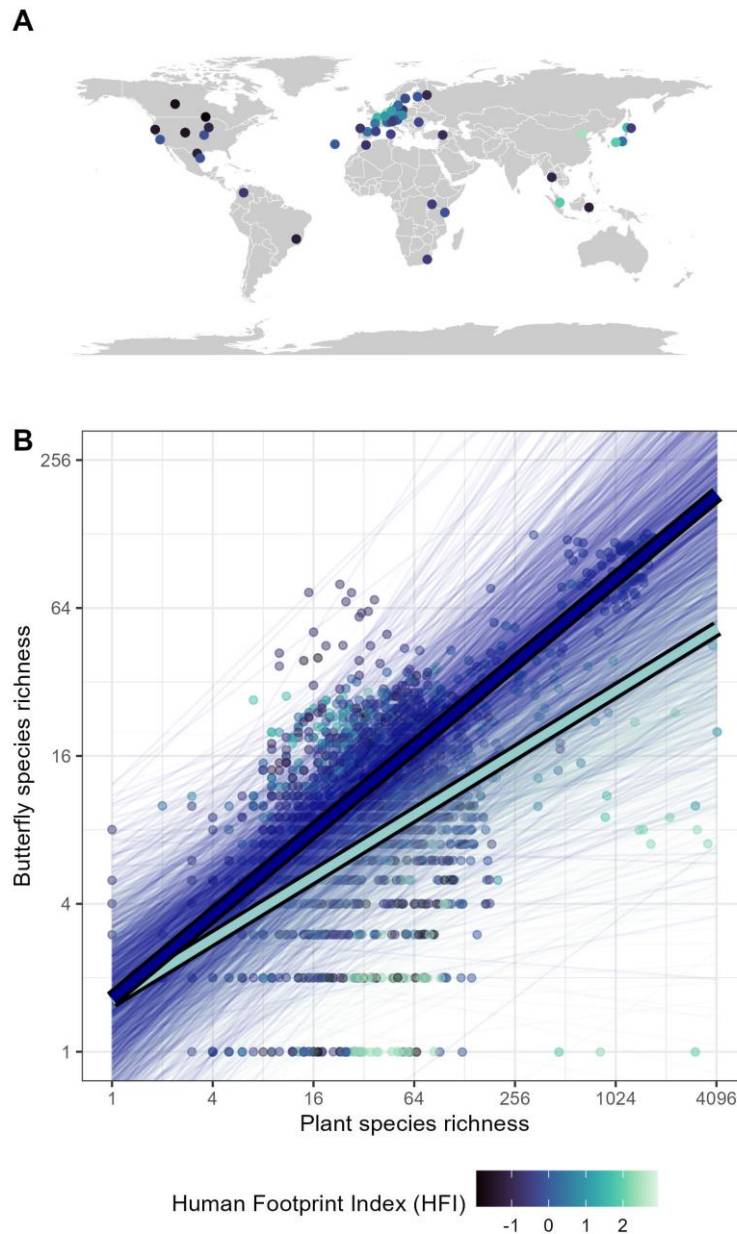
Once the model had been run, we examined the model results, by looking at the model summary, which contains a series of outputs. These included the mean (estimate), the standard deviation (Est.Errr) of the posterior distribution, the two-sided 95% Credible intervals (l-95% CI and u-95% CI) based on quantiles, the Rhat statistic (diagnostic of MCMC convergence), the Bulk effective sample size (bulk\_ESS) and the Tail effective sample size (tail\_ESS) for both group-level effects and population-effects separately. The inclusion of the bulk\_ESS and tail\_ESS in the output series was important as they allow the robustness of the model to be assessed. The bulk\_ESS assesses how well the centre of the distribution (mean or median) is resolved, and estimates the number of effective samples in the central part of the posterior distribution. The tail\_ESS evaluates the other part of the distribution by estimating the extreme quantiles and the effective sample size for interval estimates (Vehtari et al., 2021). Random effect parameters included sigma (standard deviation of the assumed normal distribution of random variables; mean values available with ranef() function). We also used functions such as stanplot() and mcmc\_plot() for visual examination of the model outputs (Bürkner, 2017, 2018).

## Results

During the study collection, we gathered a total of 56 studies. Such studies were retrieved from 5 of the 7 recognised continents, including Africa, North America, South America, Asia and Europe (Fig. 2A). Europe emerged as the continent with the highest number of studies combining butterfly and plant species richness, accounting for 27 studies or approximately 48% of the dataset. Asia followed with 12 studies, half of which were carried out in Japan. North America contributed 10 studies, and Africa provided 5, including the study of the Macaronesia islands (Canary, Madeira and Azores). South America contributed to 2 studies found in Brazil and Colombia.

In addition to the location, each study is associated with a palette of colours representing the average value of its Human Footprint Index value (Fig.2A). These colours ranged from the darkest (minimum value) to the lightest (maximum value). As a result, Europe and Asia rose as the continents with the brightest colour palettes on a global scale. The greatest human impact was recorded in countries like France and Germany in Central Europe, as well as Japan in East Asia.





**Figure 2: Earth map of the 56 selected studies (A) and Relationship between butterfly and plant species richness at minimum and maximum human impact (B).** (A) The colour gradient assigned to each study corresponds to the average values of the Human Footprint Index values in that study, ranging from the darkest (minimum value recorded, -1.94) to the lightest (maximum value recorded, 2.93). Due to the proximity of some studies, a few points slightly overlap (e.g., two studies taking place at Mount Fuji and Rocky Mountain National Park). (B) Plant species richness is represented on the x-axis, as the predictor variable, and the butterfly species richness is plotted on the y-axis as the response variable. These curve distributions allow for a visual representation of the human impact on the butterfly species richness for a specific number of plant species richness.

## **Fitness and trends of the Bayesian model**

Model convergence was appropriate based on the Rhat, Bulk Effective Sample Size (bulk\_ESS) and Tail Effective Sample Size (tail\_ESS) statistics. We found that the 4 chains from the MCMC algorithm converged well, obtaining a Rhat value of 1 for the standard variation of the model (sigma), all the entire population-level effects and most of the group-level effects. Only the standard deviation (SD) of Log2Plant with respect to the variable study.ID was different at 1.01, but not significantly different as it remained  $< 1.05$  (Vehtari et al., 2021). For all parameters, we recorded reasonable values ( $>1000$ ) for bulk\_ESS and tail\_ESS, indicating good sampling efficiency. In particular, the values for bulk\_ESS range from 1145 to 3958 and for tail\_ESS from 1627 to 2773 for each parameter (group and population level effects and sigma (Vehtari et al., 2021)).

At the level of fixed effects, we obtained for the intercept an estimate of 0.80 (95%CI: -0.87,2.36) and the estimate for Log2Plant was 0.50 (95%CI: 0.23,0.77), implying the expected increase in butterfly species richness for each unit increase in plant species richness. The estimated coefficient for human impact was 0 (95%CI: -0.33,0.32), suggesting no impact on butterfly species richness when considering it independently from plant richness. However, the log2plants\*HFI interactive term coefficient was -0.03 (95%CI: -0.09,0.03) suggesting that as the diversity of plants increases, so does the effect of HFI on the butterfly richness ~ plant richness relationship.

At the level of random effects, we found large estimate values ( $>1$ ) for the standard deviation of the intercept at the different habitats (estimate of 1.33 (95%CI: 0.40,3.54)) and study.ID (estimate of 1.79 (95%CI: 1.37,2.30)) levels. A large estimate for the standard deviation at the habitat and study level suggested considerable variation in butterfly species richness across these different variables. Certain habitats and studies would account for more or less butterfly species richness. Compared to the intercept, the model recorded smaller, but similar variations at the habitat (estimate of 0.22 (95%CI:(0.05,0.60)) and study.ID (estimate of 0.24 (95%CI:0.17,0.33)) levels.

The second part of the final figure illustrates how butterfly species richness changes in relation to both plant species richness and HFI (Fig. 2B). In the absence of human impact (dark blue line), we observed higher butterfly species richness compared to the situation with the highest human impact situation (light blue line). Furthermore, the difference between the distribution

of the minimum and maximum human impact arose as the number of plant species richness increased. This observation implies that as plant diversity increases at a given site, a greater human impact on that site would result in a greater loss of butterfly species richness. In contrast, the difference in butterfly species richness between a heavily and weakly impacted site is reduced when the number of plant species richness is lower.

## Discussion

We still know very little about biodiversity, and quantification of changes in the abundance and distribution of every species is arduous (Hortal et al., 2015). With the significant loss of biodiversity ongoing (Castagneyrol & Jactel, 2012; Novotny et al., 2002), we therefore need to develop approaches capable of informing biodiversity conservation without requiring information on the identity of each of the millions of species existing on Earth (Castagneyrol & Jactel, 2012; Mendenhall et al., 2012). Here, we propose a global analysis by applying the 'cross-taxon correlates' method, which assesses the correlation between species richness of different taxa at different sites (Dyer et al., 2007; Novotny et al., 2002) based on the biotic interactions (Castagneyrol & Jactel, 2012). In our case, considering the estimation changes in a charismatic animal group could be beneficial. Charismatic groups of animals, such as butterflies, are important for conservation purposes as they help to raise public awareness of the importance of conservation and directly protect other species living in the same ecosystem (Launer & Murphy, 1994; Seymoure, 2018; Wang et al., 2020). Beyond their charismatic appearance and umbrella grouping, butterflies play a vital role in ensuring the proper functioning of the environment through their prey and pollination actions, as well as their target prey for higher trophic levels (Both et al., 2009; Crossley et al., 2021). Relative to our stated hypotheses, results strongly support Hypothesis 2. In the face of human impact, a greater reduction in butterfly diversity will occur in relation to the diversity that would be expected based on plant diversity. Furthermore, we observed that butterfly species richness is negatively reduced when both human impact and plant diversity increase (Fig. 2B) but without human impact, our Bayesian model suggests that butterfly species richness increases with plant species richness, supporting the idea that plant diversity leads to greater animal diversity. Additionally, the difference between the lowest and the highest human impact lines widens as the number of plants increases. This study outlines an ecological scenario in which butterflies display less resilience than plants to heavily human impacted environments. This observed trend stresses

the complex dynamics brought by human impact on the relationship between two different taxa, like butterflies and plants, that are nevertheless tied by millions of years of coevolution (Ehrlich & Raven, 1964).

Highly human-influenced environments include urban areas, such as cities, and agriculture. Cities' expansion is broadly spreading in all regions of the world, with human growth estimated to reach an additional 2 billion people, most of whom will be concentrated in predominantly urban areas (Cohen, 2004; McKinney, 2006). Meanwhile, agriculture already occupies 40% of terrestrial landscapes, and increases when cities grow (van Vliet, 2019). Population growth will inevitably increase human pressure on urban biodiversity, which already faces the damages of this interaction (McKinney, 2006). In disturbed areas, several ecological processes take place, such as the invasion of alien plant species (Öckinger et al., 2009; Sing et al., 2016). As a result, plant species richness may be higher in disturbed landscapes due to the introduction of more alien plant species than alien butterfly species (McKinney, 2006; Sax & Gaines, 2003; Sing et al., 2016). However, the number of invasive species alone seems unlikely to explain the patterns we observed, which appear to reflect a higher butterfly sensitivity to disturbance.

Even with the presence of a diverse plant biodiversity in disturbed environments, butterflies may not encounter adequate environmental parameters for survival. In fact, alien plants may not serve either as good host plants for caterpillars or as effective floral food resources for adult butterflies (Buchholz & Kowarik, 2019; Concepción et al., 2015; Gaertner et al., 2017; Sing et al., 2016). The increase in invasive plants and the overall decline in the global pool of native plants could therefore play a factor in explaining why, when plant species richness increases in highly impacted environments, butterfly species richness is not commensurate. Butterflies are highly sensitive taxa, experiencing severe declines along the rural-urban gradient (Sing et al., 2016) due to their short life cycle and subtle ecological requirements (Kuussaari et al., 2021). Butterfly species richness is related to high local quality (Aguilera et al., 2019; Kuussaari et al., 2021) and connectivity (Kuussaari et al., 2021; Lizée et al., 2012), which are mainly not provided in urban environments due to the small and limited habitats offered (Kuussaari et al., 2021; Piano et al., 2020; Williams et al., 2015). The disparity between the two curves could also be explained by the high sensitivity of butterflies and the environmental filter acting on butterfly species richness in urban environments. Not all butterfly species are equally affected, highly mobile and specialist species are the butterfly species most affected by human impacts, causing a homogenisation of the species (Casner et al., 2014; Concepción et al., 2015; Eskildsen

et al., 2015; Stefanescu et al., 2004). The resulting homogenisation of species would mean that, even if the number of plants increased, the presence of additional plant-like alien species would not create a favourable environment for butterfly species, leading to the migration of butterflies or becoming extinct. With their better dispersal abilities, highly mobile species can migrate outside of human impacted areas and seek out semi-natural habitats where they thrive successfully (Concepción et al., 2015; M. S. Warren et al., 2001). As a result, homogenisation results in a greater proportion of generalist and less mobile species, with less mobile showing greater sensitivity to the presence of alien plant species (Gallien et al., 2017). Consequently, this would mitigate the ecosystem services offered by butterflies in areas of human interest across the globe (Merckx & Van Dyck, 2019; Noriega et al., 2018) and lead as an additional factor to explain our finding.

Although we worked on global data, our results are affected primarily by studies conducted in North America, Asia, and especially Europe. An equal number of studies per continent would have been preferable to get a more comprehensive trend. For example, we could not get any studies to represent Oceania, whereas this would have allowed a sixth and all continents would have been represented, as butterflies are absent from Antarctica (Gamboa et al., 2022). The disparity can be explained by the imbalance of the scientific community's distribution within environmental biology journals, where the last census in 2014 resulted in most researchers and editors being located in North America, followed by Europe, Central Asia and regions of Pacific/East Asia region (Espin et al., 2017). This editor's geographic distribution reflects the major proportion of studies collected, as Europe, North America and Asia, except for the absence of any studies in Oceania and the UK. In general, countries with the highest number of editors belong to the Global North, which groups the economically developed countries accounting for most of the world's wealth and a high capita gross domestic product (GDP). In contrast, the countries belonging to the Global South group, such as the countries of South America and Africa, resulted in only a small fraction of editors, which was reflected in our results (Espin et al., 2017).

We also lack great representation of studies present in environments where most plant and butterfly species are recorded, such as the tropical regions, because it is here especially difficult to sample both at appropriate levels of sampling completeness. Over 90% of butterfly species are found in the tropics (Pinkert et al., 2022), and between 50,000 and 120,000 species of vascular plants occur in the three main tropical regions, i.e. Latin America, the Afrotropical

region and Southeast Asia (Bonebrake et al., 2010; Raven et al., 2020). For example, of the 12 studies collected in Asia, we only recorded 4 studies in the Asian tropics (Thailand, Indonesia and Singapore), 3 studies (Kenya, South Africa and Uganda) out of 5 in Africa and an overall total of 2 studies in South America (Colombia and Brazil). Furthermore, the addition of Madagascar could also strengthen the representation in the Afrotropical regions as the island accounts for 16.98% and 7.24% of vascular and butterfly species richness respectively in the Afrotropical region (Raven et al., 2020). The small number of studies reported in tropical regions is not surprising; in fact, little is known about butterflies living in the tropics compared to butterflies in temperate environments. This is partly due to the scarcity of data and the lack of resources dedicated to science in tropics regions, even though butterflies belong to one of the most known taxonomically and ecologically group of insects (Bonebrake et al., 2010; Espin et al., 2017; Thomas, 2005). In addition, monitoring butterflies and plant species in tropical environments presents be challenging due to the wide range of species and the complexity of the habitat, as the canopies' height up to 60 m above the ground (Bonebrake et al., 2010; Checa et al., 2022; Vizentin-Bugoni et al., 2018). However, despite the lack of data on other continents and in tropical environments, apart from Europe, we consider that our dataset includes a substantial number of studies (>50), encompassing different landscapes and continents in regards to a conservation purpose study.

In this way, our study highlights the importance of using systematic reviews on the field of conservation biology with the finding that a charismatic animal indicator as butterflies, exhibit greater sensitivity to human impact. We were able to draw a global pattern on one of the animals that contributed greatly to understanding of conservation, ecology and evolution (Boggs et al., 2003; Bonebrake et al., 2010; Gilbert & Singer, 1975). These results highlight the priority of conserving butterflies on a global scale, particularly in environments impacted by human activity as categorised by the human footprint index, such as built-up environments, population density and other derived human activities such as crop and pasture lands and transport routes (railways and waterways) (Venter et al., 2016, 2018). Therefore, we highlight the relevance of a global finding using a cross-taxon correlation method combined to an ecological review, which could enhance future studies analysing global trends or on more restricted areas (e.g. countries or a continent) of butterflies or other animal groups interdependent with plants that may be underestimated in conservation in order to push further guidelines if data availability is present. For example, Europe and Asia represent the regions in our finding with the most HFI values recorded, suggesting a heightened impact on butterflies decline in these areas. Given the

hypothesised explanations for the decrease in butterflies, we encourage further studies in these regions examining how the eradication of alien plant species by replacing them with native plant species (i.e., plant species belonging to the keystone plant genera (Narango et al., 2020)) in high plant species richness sites could influence butterfly species richness, as the eradication of alien plant species has proved effective for butterflies communities (Florens et al., 2010; Hanula & Horn, 2011). Finally, by emphasising how the HFI metric aligns with the main threats butterflies face such as habitat loss and degradation, we encourage further research into the impacts on butterfly species in areas of high human impact. This would lead to a better understanding of their responses and the implementation of appropriate new conservation measures, such as in large cities that comprise the categories in the HFI and lead to a severe and biotic homogenization of habitat for this group.

## Conclusion

In conclusion, our study aligns with previous findings indicating a general decrease in continents such as Europe (M. Warren et al., 2021) and North America (Sánchez-Bayo & Wyckhuys, 2019; Wepprich et al., 2019), and suggesting that butterflies appear to be more sensitive to human impacts than plants, a fact that was shown here based on a global-scale data synthesis. Our study highlights the importance of open data and systematic reviews in ecology and conservation (Pullin & Stewart, 2006). Without the need to perform a field survey, we were able to draw a global pattern on one of the animals that contributed greatly to understanding of conservation, ecology and evolution (Boggs et al., 2003; Bonebrake et al., 2010; Gilbert & Singer, 1975). Our study supports particular care for butterfly conservation in areas sensitive to high levels of human disturbance and biotic homogenization, such as large cities (Concepción et al., 2015; Hunter, 2007; Kuussaari et al., 2021; McKinney, 2006; Riva et al., 2023) and anthropogenic landscapes (Riva et al., 2018, 2020). We recommend an increase in studies conducted in the tropics to enhance our understanding of how butterflies respond to anthropogenic disturbance in comparison to plants. This approach would contribute to the establishment of appropriate conservation measures, in line with previous studies showing how highly mobile and specialist species are disproportionately impacted in urban environments and how less mobile species are more vulnerable to disturbance (Concepción et al., 2015; Lososová et al., 2012; Riva et al., 2023; Sing et al., 2016).

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