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Identifying biodiversity hotspots over time: Stability, sampling bias, and conservation implications

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ABSTRACT

The conservation of biodiversity is a major challenge facing society. In order to design effective conservation strategies, we must be able to identify the areas in which biodiversity is concentrated (i.e., biodiversity hotspots). However, observed patterns of species richness are often heavily biased by sampling effort, undermining the reliability of hotspot detection. Therefore, it is important to understand how the location of identified hotspots varies over time as knowledge about the identity and distribution of species increases. Using what is likely the most comprehensive insect database in the world (the butterflies of Great Britain), we examine the survey effort achieved over time, estimating the degree of congruence in the identification of butterfly biodiversity hotspots at different time intervals. This congruence is low over much of the 215-year period studied, remaining so for hotspots based on a rarity metric even after 1980, when the inventories were already relatively complete. The location of hotspots based on species richness has been more stable in recent decades, reflecting one the more complete sampling coverage in these years. These results highlight the risk of misidentifying biodiversity hotspots based on inadequate data and point to the need for greater sampling effort for insects to improve inventories before identifying and proposing areas for conservation. This study has significant implications for biodiversity conservation, as it provides insights into the usefulness of identifying priority areas based on incomplete inventories, such as those we currently have worldwide.

1. Introduction

There is increasing scientific evidence showing that biodiversity loss compromises human well-being (Cardinale et al., 2012; Marselle et al., 2021) and is becoming one of the foremost challenges facing humanity (Dirzo et al., 2014). This process of biodiversity loss, through which unique organisms, many of which have yet to be described, are disappearing (Cardoso et al., 2020), threatens essential ecosystem services (Costanza et al., 2014). It has been described as the Earth's sixth mass extinction event (Ceballos et al., 2017; Cowie et al., 2022) and is disproportionately affecting invertebrates, the least understood animal group from taxonomic and

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biogeographical perspectives (Boyle et al., 2024), and which also represents the largest proportion of known Earth's biodiversity (Schuldt and Assmann, 2010). Invertebrates in general, and insects in particular, inhabit all types of environments, both terrestrial and aquatic (Leandro et al., 2017), playing key roles in numerous ecological processes (Schuldt and Assmann, 2010), such as decomposing organic matter and pollinating more than 75 % of flowering plants (Ollerton et al., 2011). Despite their critical importance, however, invertebrates have received limited attention in environmental conservation policies and have largely been omitted from land management strategies (Pryke et al., 2024).

In the absence of a comprehensive strategy to mitigate the impact of anthropogenic processes globally, the creation and maintenance of protected areas in regions recognised for their uniqueness or species richness is a major tool for conserving biodiversity (Watson et al., 2014). Numerous conventions and international initiatives aim to expand globally protected areal coverage, as acknowledged at the 15th Conference of the Parties to the Convention on Biological Diversity held in 2022, where a historic global biodiversity agreement was adopted to protect 30 % of the Earth's land and water by 2030. This goal of expanding the network of protected areas can be pursued by optimizing the geographical and environmental representativeness of potential protected sites and enhancing the representativeness of species and populations that we aim to safeguard for the future (Margules and Pressey, 2000). However, the effective use of biodiversity information in conservation planning (Eckert et al., 2023) relies heavily on the availability of data regarding the identity and distribution of most species (Linnean and Wallacean shortfalls; Lomolino and Heaney, 2004; Vergara-Asenjo et al., 2023). Consequently, conservation efforts have traditionally been skewed towards vertebrates and vascular plants, while invertebrates have received considerably less attention due to the limited availability of information (Clark and May, 2002). This knowledge gap is especially evident for insects and in highly diversified regions such as tropical or Mediterranean areas. Data held in the Global Biodiversity Information Facility (GBIF), the largest existing database on global biodiversity, provides an example of these knowledge gaps. An examination of around 22 million GBIF records covering c. 300,000 species indicate that only 0.5 % of the Earth's surface could be considered well-sampled for insects (García-Roselló et al., 2023). Another example is provided by a recent analysis of nearly 750,000 Iberian records of around 2250 insect species (Sánchez-Fernández et al., 2022). This revealed that, despite decades of taxonomic and faunistic work, the existing information is so scarce and biased that it hampers our ability to obtain a reliable picture of biodiversity patterns on the Iberian peninsula. This, in turn, limits our capacity to identify key areas for conservation.

The biases and gaps in insect biodiversity data mean that species richness maps often closely resemble maps of sampling effort, such as the number of records per spatial unit (Hortal et al., 2007). Indeed, it has already been demonstrated that there is a clear relationship between observed richness patterns and sampling effort (Dennis and Williams, 1986; Oliveira et al., 2017; Hughes et al., 2021). In other words, many areas identified as biodiversity hotspots and proposed as conservation priorities may not be those most appropriate for protection, but rather the most extensively studied sites. The dynamic nature of species distributions, responding to recent and intense climatic and environmental changes, further complicates the delimitation of protected areas based on species distribution data (Thomas and Gillingham, 2015). Consequently, inventory completeness values at some locations fail to stabilize over time due to the continual addition of new species in response to climate change (Sánchez-Fernández et al., 2021). The sampling challenge is more prevalent during the early stages of accumulating taxonomic and distributional information, while dynamic distribution change is increasingly relevant as climate change accelerates. However, both of these difficulties pose significant challenges when designing networks of protected areas. It is, therefore, beneficial to understand how much the identification of hotspots fluctuates as additional biodiversity information becomes available over time. If selected areas remain largely consistent and the impact of climate change on the target group is minimal, the initial faunistic knowledge may have been sufficient to accurately identify important biodiversity areas. Conversely, if identified hotspots shift significantly as sampling effort intensifies over space and time, decisions based on available data at any given time may prove inadequate, especially if species distributions are highly dynamic in response to climate change.

Of course, these scenarios represent extremes, and there is likely a continuum of conditions in which temporal variation in the location of identified hotspots may be more or less pronounced. Estimating the magnitude of this variability could help determine how far we are from implementing an effective conservation strategy based on the selection of priority areas. Addressing this question is challenging, as it requires an exhaustive database where sampling effort over time is intense and prolonged across a wide territory. Such data would provide a reliable representation of "true" biodiversity patterns, clearly illustrating the temporal variation in the delimitation of hotspots. For insects, studying this issue is particularly difficult, as only a few countries with a long, popular tradition of natural history study, such as Great Britain, have been able to generate such comprehensive databases (Sánchez-Fernández et al., 2021). The database that compiles much of the information on the distribution of British butterflies is probably the most complete for any insect group worldwide, with more than 10 million records covering 58 native butterfly species over a period of more than 200 years. In this study, we assume that the contemporary image from this database reflects the "true" distribution pattern of butterfly biodiversity in Great Britain, and we aim to examine how a hypothetical selection of hotspots might have varied over time. To this end, we identify the hotspots using the entire dataset, then determine these same hotspots using ten-year data intervals, to finally calculate the degree of overlap between the identified hotspots over time. Based on these results, we discuss the utility of identifying priority areas from incomplete inventories.

2. Material and methods

2.1. Study area and database

The British butterfly database contains a total of 10,046,366 records from 58 species belonging to the families Hesperidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae, and Riodinidae, for the period 1800–2014. In our analyses, only resident species

were considered, but *Phengaris arion* (Linnaeus, 1758) was excluded due to the existence of a long-term reintroduction programme. *Vanessa atalanta* (Linnaeus, 1758) was included, as it now appears to be a year-round resident species in Britain (Fox and Dennis, 2010). This database was generated by the “Butterflies for the New Millennium” project, managed by Butterfly Conservation (<https://butterfly-conservation.org/>). The project began in 1995 but has accumulated a substantial volume of historical records (Fox et al., 2015), including those used to produce the first butterfly atlas for Britain and Ireland (Heath et al., 1984). The Butterflies for the New Millennium database primarily consists of butterfly presence records (unique combinations of species \times recorder \times location \times date) collected from opportunistic and non-standardised surveys conducted mainly by citizen scientists and amateur naturalists. These records were either submitted directly to the project or sourced from platforms such as *iRecord*. Additionally, this database includes data from structured and standardised surveys conducted under the UK Butterfly Monitoring Scheme. Before being incorporated into the database, all records were verified by a network of taxon experts. For this analysis, the records were grouped into specific species/year/10 km \times 10 km grid square combinations, divided into twenty-two cumulative intervals starting from 1800, each progressively adding approximately a decade (i.e. 1800–1810, 1800–1820...1800–2010, and 1800–2014). The original reference system of the database is Ordnance Survey’s British National Grid (EPSG: 27700), which was transformed into geographic coordinates (latitude/longitude) according to the World Geodetic System (WGS84).

2.2. Estimation of sampling effort and identification of well-surveyed grid cells

To map the geographical variation in sampling effort and identify areas with relatively complete inventories for each considered period, the R package *KnowBR* (Guisande and Lobo, 2019; Lobo et al., 2018) was used. This package generates accumulation curves that reflect the increase in the number of species as sampling effort intensifies across all spatial units within a given territory. The number of records in the database was used as a proxy for sampling effort. The analyses were conducted at two different spatial unit resolutions: 5-minute ($n = 2775$) and 30-minute ($n = 209$) grid cells (approximately 10 km \times 10 km and 50 km \times 50 km, respectively). A record-by-species matrix was built and used to estimate the accumulation curve for each cell based on the exact estimator of Ugland et al. (2003). Since species accumulation curves depend on the order in which samples are added, this author developed an analytical method to generate the exact cumulative number of species, avoiding costly randomization procedures. The resulting smoothed accumulation curve was then fitted to a rational function (Flather, 1996) to estimate asymptotic values. In our case, these values represent the expected number of species as sampling effort approaches infinity. The ratio between the observed number of species in each cell and the predicted number, as estimated by the accumulation curve, allows for the calculation of completeness for each grid cell. Additionally, the final slope of the accumulation curve indicates the rate of species increase with the addition of new records. These completeness and final slope values help distinguish cells with reliable inventories from those that are insufficiently surveyed, using a predefined threshold. In our case, cells with completeness values of 90 % or higher, and slope values of 0.01 or lower

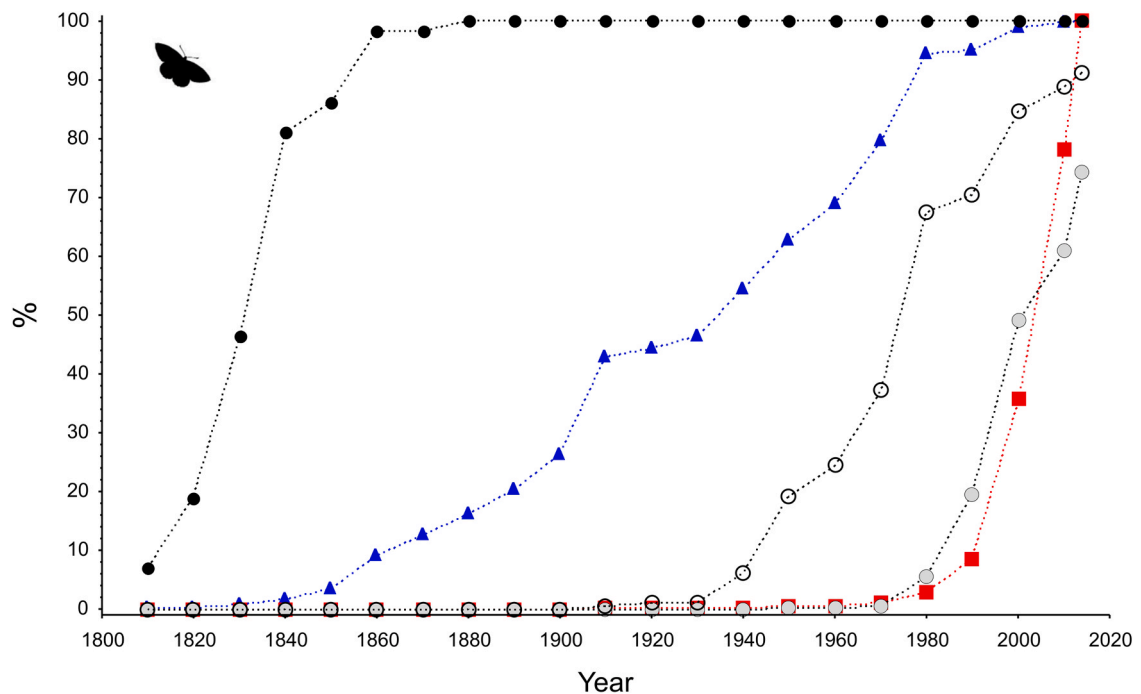


Fig. 1. Increase over time in the accumulated percentage of i) number of species recorded in Great Britain (black dots), ii) cells (at 5-minute resolution) with butterfly records (blue triangles), iii) database records (red squares); iv) cells (at 5-minute resolution) that can be considered well-surveyed (grey circles), and v) cells (at 30-minute resolution) that can be considered well-surveyed (open circles).

(indicating the addition of one new species to the inventory for every 100 new records), are considered well-surveyed (see Lobo et al., 2018).

2.3. Hotspot selection over time

Both species richness (i.e., the number of species) and the geographic rarity of each cell were used to identify hotspots across different periods of accumulated years. Rarity was determined as the average of the rarity values of the species occurring in each cell (sum of the rarity values divided by the number of species). The rarity value of each species was calculated as the inverse of the number of 10 km x 10 km cells occupied by that species during each period considered ($1/n$; where n represents the number of UTM squares in which the species appears) (Rey Benayas and De La Montaña, 2003). Once these two values were calculated for each cell, the cells with the highest species richness or rarity were selected, using the 1st and 10th percentiles as cut-off points (i.e., the top 1 % and 10 % of cells with the highest values). To estimate the degree of temporal congruence between hotspots, the identity of the 10 km x 10 km cells selected in each period was first identified (22 sets of cells, one per period). Then, the percentage of shared cells between each period and those selected using the accumulated information until 2014 was calculated.

3. Results

3.1. Survey effort and identification of well-surveyed cells

During the first period, between 1800 and 1810, there are only five records corresponding to four different species, distributed across five distinct grid cells. By 1860, the species inventory rapidly incorporated more than 95 % of the species inhabiting the entire territory, although the records were concentrated in just 10 % of the study area (5-minute grid cells). At that point in time, the number of records represented just 0.01 % of the total records accumulated in the database (Fig. 1). It was not until 1940 that faunal information became available for more than half of all the 5-minute cells. However, at that time, only 6 % of the total 30-minute cells and not one 5-minute cell could be considered well-surveyed according to the selected criteria. It was not until 1980 that more than half of the 30-minute cells could be identified as well-surveyed, with half of the 5-minute cells being considered well-surveyed by around the year 2000. Since 1940, the growth in the number of well-surveyed 30-minute cells follows a linear trend, with a rate of 2.6 cells per year ($t = 13.80$, $p < 0.001$, $R^2 = 0.97$). In the case of 5-minute cells, this linear increase begins in 1970, at a rate of 48.6 cells per year

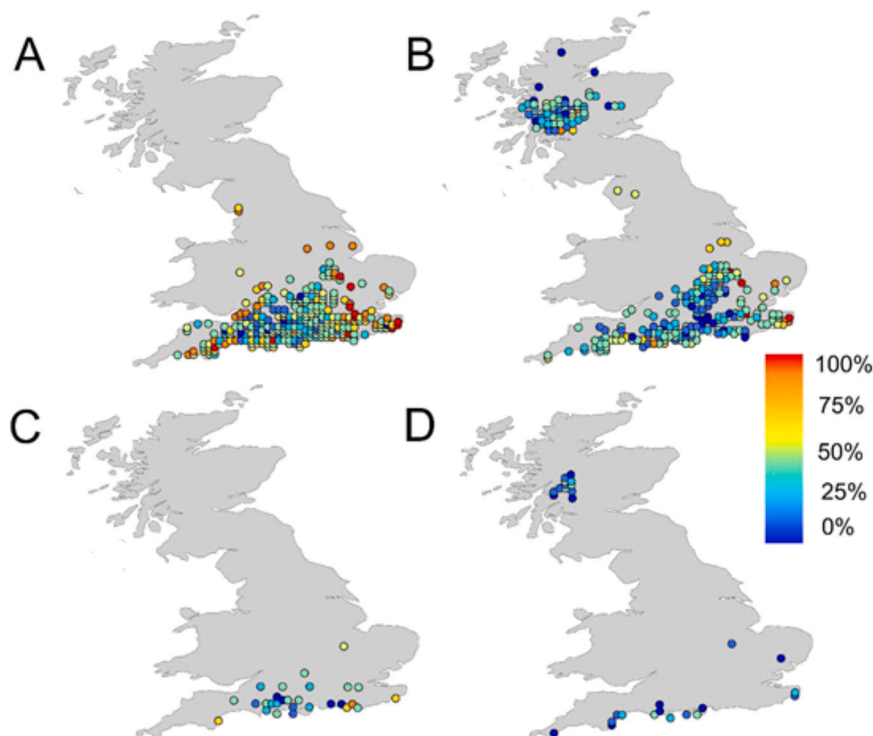


Fig. 2. Maps representing the location of the species richness and rarity hotspots for British butterflies according to the complete information provided by the Butterflies for the New Millennium database (1800–2014) (A = 10 % of cells with the highest species richness values; B = 10 % of cells with the highest rarity values; C = 1 % of cells with the highest species richness values; D = 1 % of cells with the highest rarity values). Colours of the dots represent the percentage of occasions that each 10 km x 10 km cell has been selected as hotspot along the different temporal considered time periods.

($t = 9.77$, $p < 0.001$, $R^2 = 0.96$). In the last year considered (2014), approximately 91 % of the 30-minute cells and 74 % of the 5-minute cells were considered well-surveyed, even though there are database records for all these cells.

3.2. Hotspot selection

Species richness hotspots, based on the complete information from the database, are concentrated in the south of Great Britain, primarily in the South West and South East England regions, but also in a few grid cells located in the East Anglia and East Midlands regions (Fig. 2). However, the rarity approach identifies a significant portion of hotspots being located in Scotland (Fig. 2).

The top 1 % of cells with the highest species richness values, using the complete database, were on average also selected in about a third of the 21 time periods (33.1 %; maximum = 73.9 %; minimum = 4.4 %) (Fig. 2). This percentage increases slightly (to 45.4 %) when considering the top 10 % of cells with the highest species richness (maximum = 91.3 %; minimum = 4.4 %). In the case of rarity, the top 1 % of cells with the highest rarity values are rarely selected in other periods (mean = 17.9 %, maximum = 47.8 %; minimum = 4.4 %), though they are selected in about a third of cases when the top 10 % of rarity cells are considered (mean = 33.1 %, maximum = 87.0 %; minimum = 4.4 %) (Fig. 2).

Using species richness as the criteria to delimit hotspots, just half of the selected cells (top 1 %) until 1950 are shared with those finally selected with the full dataset (Fig. 3A). For the top 10th percentile of cells with higher species richness values, this year was 1920 (Fig. 3B). From these points onwards, the percentage of shared cells increases linearly by about 7 % per decade for the top 1st percentile of cells, and around 6 % for the top 10th percentile. In the case of rarity, the congruence between the selected cells at each temporal interval and the final selected hotspots is much lower. Indeed, only 10 % of cells (top 1st percentile) included in the final selection hotspot using rarity match with those selected in 1970 (Fig. 3C). From that point onwards, the increase is rapid and consistent at 21 % per decade. The pattern for the top 10th percentile of cells is relatively similar, although the number of shared species is always higher (Fig. 3D).

4. Discussion

We have identified that hotspot locations shift in relation to sampling intensity and data density. The degree of spatial congruence between hotspots identified over time is low, particularly when a very restrictive threshold is used to select these areas, and especially when the rarity criterion is applied. For instance, the percentage of overlap between hotspots identified in 2014 and those identified in 1980 is approximately 70 % for areas considering the top 1st percentile of cells with the highest species richness values. However, this overlap drops to just 20 % when focusing on the top 1st percentile of cells with the highest rarity values. It is noteworthy that by 1980, species inventories already demonstrated a significant degree of completeness, with around 67 % completeness for the top 10th percentile of cells with the highest species richness values, but only 7 % completeness for the top 1st percentile of cells. The pattern

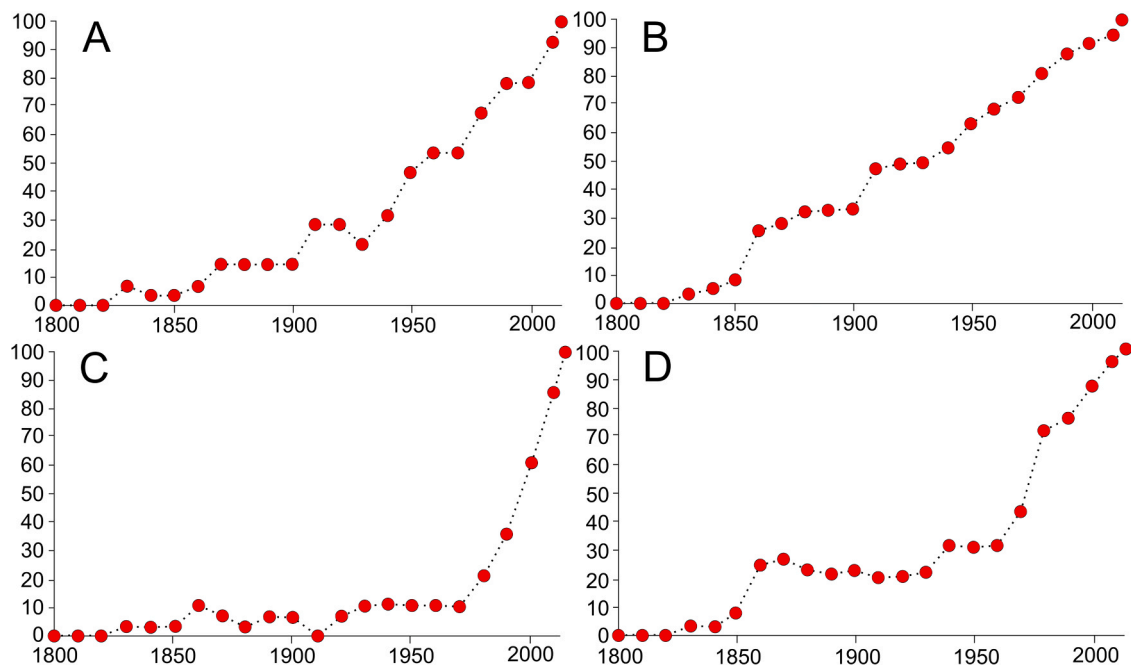


Fig. 3. Variation in the percentage of 10 km x 10 km cells identified in 2014 (all data) and those identified in each one of the considered temporal scenarios. A = 1 % of cells with the highest species richness values; B = 10 % of cells with the highest species richness values; C = 1 % of cells with the highest rarity values; D = 10 % of cells with the highest rarity values.

observed prior to this date is comparable to the current state of insect databases in many regions with different climatic conditions (Ballesteros-Mejía et al., 2013; Sánchez-Fernández et al., 2022; Belhaj et al., 2023; Wang et al., 2025). In the case of British butterflies, the deficiencies observed prior to 1980 are unsurprising, as the first coordinated recording scheme was only initiated at 1976/1977. Data from earlier periods represent a fragmented, taxonomically biased, and retrospective collation of records, rather than an accurate reflection of what recorders were actively documenting at the time. An example of this is provided by a recent study of historical *Carterocephalus palaemon* records in England: the Butterflies for the New Millennium database contained 266 such records of this scarce species, but searches of published texts, recorders' notebooks and collections, added over 3500 historical records (Wildman et al., 2022).

Considering the accumulation of British butterfly records up to 1980, one might expect a higher degree of overlap in hotspots identified using the full database. Unfortunately, the results obtained suggest that even insect databases capable of compiling a large number of records—achieving percentages of spatial units with reliable inventories of around 50 % at a moderate resolution (e.g., 50 km x 50 km)—are unlikely to provide reliable representations of hotspot locations. From a broader perspective, it is important to note that the majority of biodiversity databases worldwide are still in the early stages of data compilation (Ball-Damerow et al., 2019). This raises significant concerns about the reliability of prioritised conservation area selections based on most of insect inventories currently available.

These changes in the identity of hotspots indicate that the focus of inventory efforts shifts over time, with new hotspots emerging in relatively unexpected locations as sampling effort intensifies and expands. The generally low levels of overlap in hotspot areas over time can be attributed to the very patchy selection of records during earlier decades, spatially biased sampling in subsequent years (Dennis and Thomas, 2000; Isaac and Pocock, 2015; Sánchez-Fernández, et al., 2021), and, importantly, the dynamism in species' geographical distributions as they respond to climate change (Dennis and Shreeve, 1991; Menéndez et al., 2006; Mair et al., 2014). The initial spatial concentration at the beginning of the inventory process gradually gives way to broader coverage of sampled sites, which inevitably facilitates the detection of "true" hotspots. During the early decades, the number of records in the Butterflies for the New Millennium database is very low, but by 1970, the dataset shows a marked increase in sampling intensity, particularly when considering the 5-minute grid cells. This shift in the 1970s and 1980s reflects the adoption of new methodologies and an increase in sampling effort, progressively improving the completeness of the cells, which reached 50 % by the year 2000. This process of revealing the reality of biodiversity distribution is particularly challenging in the case of rarity, for several reasons. Firstly, incomplete spatial sampling coverage poses a greater obstacle for species with limited geographical distributions, especially as the geographical pattern of rarity is more complex. Moreover, rarity values depend on the relationships between the distribution of rare species and the distribution of the recording effort, as well as on whether rare species remain rare as survey effort increases. Species traits can also influence biodiversity inventory processes, affecting the assessment of species richness and rarity. In the British butterfly database, common and highly detectable species were underrepresented in the early stages but over-sampled in later periods. Early entomologists primarily sought to assemble comprehensive collections, at least at a broad scale, prioritizing the discovery of new records over repeatedly collecting the same species. Conversely, in later stages, the adoption of standardized transects as quantitative sampling methods likely led to the overrepresentation of common and easily detectable species (Lobo et al., 2021). While this bias could hinder the accurate identification of biodiversity hotspots, particularly when based on species richness, the conservation implications of misidentifying areas with the highest biodiversity may be mitigated. This is because the species contributing to changes in species richness in specific cells (i.e., those recorded towards the end of the inventory process) are generally widely distributed species with lower conservation interest (Fox et al., 2022).

There is an urgent need to take decisive action to prevent the extinction of insects (Cowie et al., 2022). However, action cannot, and should not, wait for the existence of reliable, accessible and sufficiently comprehensive datasets capable of facilitating the effective design of conservation strategies (García-Roselló et al., 2023). Our results, using what is likely the most comprehensive database on a prominent group of insects, indicate that a prolonged, sustained effort over time is required to achieve representative coverage of reliable inventories. It is also evident that selecting protected area networks on far less complete pictures of biodiversity distribution run a serious risk of failing to conserve true hotspots. Moreover, even an extensive and well-resourced effort, such as that for British butterflies, does not guarantee that the selection of hotspots will be entirely accurate. The dynamic nature of species distributions, along with the accelerated changes in climatic and environmental conditions driven by human activities, makes any decision regarding areas to be protected provisional (see Arneth et al., 2020; Sánchez-Fernández, et al., 2021). This situation highlights the need i) for mechanisms to continuously monitor biodiversity, ii) for the coordinated application of various conservation strategies, and iii) to consider future climate-driven range shifts when selecting protected areas today. So, what can be done in such a scenario? We suggest that, although it may not be the ideal option, the existing information should be used to take immediate conservation actions. However, we also emphasise the importance of developing well-designed and standardised sampling efforts to produce up-to-date and representative inventories.

Future conservation efforts could benefit from integrating butterfly hotspot data with information from other well-studied taxa, such as vertebrate data, to identify multi-taxa biodiversity hotspots that more comprehensively reflect broader biogeographical patterns. Moreover, our findings underscore the challenges of identifying hotspots in regions with limited biodiversity data, highlighting the need for increased sampling efforts to ensure the reliability of conservation prioritization in less well-studied geographic areas. The accurate description of biodiversity patterns is essential not only for the conservation of individual species but also for the protection of the ecosystem services upon which we depend. Biodiversity loss represents a significant threat to ecological stability and human well-being (Cardinale et al., 2012), and a concerted effort is needed to mitigate its impact and promote global sustainability.

Ethical statement

This research was conducted in accordance with applicable legislation and ethical standards.

CRedit authorship contribution statement

D. Sánchez-Fernández: Conceptualization, Methodology, Validation, Writing – Original Draft, Writing – Review & Editing, Visualization; **A. Jiménez-Jiménez:** Methodology, Writing – Review & Editing; **R. Fox:** Methodology, Validation, Data Resources, Writing – Review & Editing; **R.L.H. Dennis:** Methodology, Validation, Data Resources, Writing – Review & Editing; **J.M. Lobo:** Conceptualization, Methodology, Validation, Writing – Original Draft, Writing – Review & Editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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Data availability

Data will be made available on request.

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