




Extensive mismatch between protected areas and biodiversity hotspots of Iranian Lepidoptera

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Abstract

1. Amidst the era of rapid decline in insect diversity, the role of protected areas (PAs) in conserving current insect diversity is more significant than ever. Previous studies indicate that the species-diverse regions in Iran fall within two global biodiversity hotspots (GBHs): the Irano-Anatolian hotspot in the north and the Caucasus hotspot in the west. However, there is an extensive conservation gap between species-diverse regions and PAs for different vertebrate taxa. Additionally, mega-diverse groups of insects have been overlooked in previous conservation assessments.
2. In this study, using the most comprehensive occurrence dataset of 1974 species from nine families of Lepidoptera, we delineated regions with statistically significant high diversity as diversity hotspots of the group. Furthermore, we defined the regions with higher conservation priority. Finally, we applied a gap analysis to assess the mismatch between the network of PAs and the most species-diverse regions.
3. Most species-diverse regions of Lepidoptera fall within GBHs and particularly the Irano-Anatolian hotspot. Overall, the results of our gap analysis revealed that less than one quarter of currently established PAs cover priority areas for conservation, which indicates a dramatic deficiency of the network of PAs in conserving higher priority areas of Lepidoptera.
4. Misplacement of the PAs in Iran, beside pressure of human footprint, can reduce the effectiveness of the established PAs to conserve the current biodiversity. Hence, enhancing the existing network of PAs and designing new ones, while considering mega-diverse taxa such as insects, will be essential for implementing effective conservation practices.

KEYWORDS

biodiversity hotspots, endemic centres, Macroheterocera, protected areas, Rhopalocera

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INTRODUCTION

Insect populations are dramatically declining worldwide (Blüthgen et al., 2023; Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020). Anthropogenic factors like overexploitation, agricultural intensification, habitat destruction and climate change are among the main reasons for this drastic deterioration (Maxwell et al., 2016; Pimm et al., 2014; Shivanna, 2022). Protected areas (PAs) networks are expected to serve as bulwarks against the negative impacts of human-induced activities (Maron et al., 2018; Pringle, 2017; UNEP-WCMC & IUCN, 2021). However, only iconic and flagship species, mainly mammals and birds, are usually considered in the initial design of PAs, whereas megadiverse taxa of invertebrates are largely overlooked and ignored (Chowdhury et al., 2022; D'Amen et al., 2013; Dias-Silva et al., 2021; Nóbrega et al., 2011; Verissimo et al., 2011). Furthermore, human interests in specific areas often prevented their protection, leading to a frequent misplacement of PAs (Le Saout et al., 2013; Venter et al., 2018; Visconti et al., 2019). According to Chowdhury et al. (2022), only a few studies have reported effective placement of PAs over regions of high insect diversity globally. Additionally, growing evidence shows that these last refugia are under high pressure by human habitat modification and climate change (Karimi & Jones, 2020; Laurance et al., 2012; Visconti et al., 2019). Therefore, there is an urgent need to assess the effectiveness of these networks and upgrade them towards conserving mega-diverse groups such as insects.

Defining and designing PAs for protecting species-diverse regions requires good knowledge of distribution patterns of biodiversity and identifying biodiversity hotspots (Kati et al., 2004; Marchese, 2015). Preserving as many species as possible by minimizing conflict with human activities is one of the most cost-effective strategies to protect biodiversity (Brooks et al., 2004; Brooks et al., 2006; Kati et al., 2004; Pringle, 2017). Globally, 36 global biodiversity hotspots (GBHs) were delimited based on high rates of endemism and high threat level of vascular plants covering 16% of the terrestrial areas (Critical Ecosystem Partnership Fund, 2016; Mittermeier et al., 2011; Myers et al., 2000). Defining these regions has been an attempt to provide a framework for concentrating conservation practices on higher priority areas (Brooks et al., 2006; Mittermeier et al., 2011; Myers et al., 2000). However, these biodiversity hotspots are also under high pressure due to human-induced threats (i.e., agricultural intensification, climate change, etc.) and have lost a significant amount of their natural habitats (Bellard et al., 2014; Habel et al., 2019). Considering that biodiversity is unevenly distributed, GBHs cover a wide range of areas extending over the territories of many countries (Cañadas et al., 2014). Detecting hierarchical nested biodiversity hotspots within GBHs will be an important planning tool to define higher priority areas for conservation: the area with a high rate of irreplaceability and vulnerability within coarse scaled GBHs (Bacchetta et al., 2012; Brooks et al., 2006; Cañadas et al., 2014; Ferrier et al., 2000; Le Saout et al., 2013; Noroozi et al., 2018; Pressey et al., 1994). A biodiversity hotspot of lower hierarchical level can be defined at a finer scale (e.g., at nano-, micro-, meso-scale, etc., as suggested by Cañadas et al.

(2014)) based on criteria such as species richness, endemism and vulnerability of the region (Lamoreux et al., 2006; Pascual et al., 2011; Qian et al., 2023). These finer scaled priority areas provide achievable targets for effective conservation efforts.

Countries around the world have committed to develop the network of PAs by 17% of their terrestrial land by 2020 (Aichi Target 11, established by the Convention on Biological Diversity [CBD]) and by 30% by 2030 (under post-2020 Global Biodiversity Framework; Butchart et al., 2015; Chandra & Idrisova, 2011; Farhadinia et al., 2022; Joppa et al., 2011). Although there are substantial advances towards meeting these targets, most countries will likely not fulfil their commitments (Farhadinia et al., 2022; Joppa et al., 2011; Watson et al., 2014). In comparison with other continents, despite higher biodiversity, Asia is the most underperforming as only 40% of the Asian countries met the target of 17% (Farhadinia et al., 2022). Considering the expansion rate of the PAs in Asian countries, it would be unlikely for them to achieve the target of 30% coverage by 2030 (Farhadinia et al., 2022; Visconti et al., 2019).

In southwest Asia, two GBHs extend across the northern and western parts of Iran: the Irano-Anatolian and the Caucasus hotspots (Critical Ecosystem Partnership Fund, 2016; Myers et al., 2000; Mittermeier et al., 2011; Figure 1). While the Irano-Anatolian hotspot covers mountainous areas of the north and west of the country, the Caucasus mainly encloses a narrow area across the southern seashores of the Caspian Sea (Mittermeier et al., 2011; Myers et al., 2000). Independent studies indicate that the most species-diverse regions of flora and fauna for the country are distributed across two main mountain ranges of Alborz in the north and Zagros in the west (Farashi et al., 2017; Noori et al., 2021; Noroozi et al., 2018; Noroozi et al., 2019; Yousefi et al., 2022; Yousefi et al., 2023; Yusefi et al., 2019). These mountain ranges (Mountains) almost overlap with the two GBHs, particularly the Irano-Anatolian. On the other hand, some studies highlighted areas with significant rates of endemism and species richness outside GBHs across mountainous areas of the northeast, south and southeast regions (Noori et al., 2021; Noroozi et al., 2018; Noroozi et al., 2019; Yousefi et al., 2022). Previous studies revealed significant conservation gaps across the species-diverse regions of endemic and threatened species for well-known taxa such as mammals, birds and plants (Farashi & Shariati, 2017; Ludovicy et al., 2022; Noori et al., 2021; Noroozi et al., 2019; Yousefi et al., 2022; Yusefi et al., 2019). However, there is a substantial deficiency of studies concerning the conservation status of understudied taxa, such as invertebrates and particularly insects, to investigate the effectiveness of the current network of PAs.

Lepidoptera are considered one of the most species-rich taxa in Iran with at least 4812 species in this country (Rajaei & Karsholt, 2023; Rajaei, Noori, et al., 2023; Rajaei, Aarvik, et al., 2023; see Table 1). Landry et al. (2023) estimated that over 9000 lepidopteran species in total may occur in Iran. The known species belong to 70 families with at least 892 endemic species (19.7%; Rajaei, Noori, et al., 2023; Rajaei, Aarvik, et al., 2023). The rate of endemism among the well-studied families ranges from 9.4% for Pieridae to 46% for Zygaenidae (Table 1; Rajaei, Noori, et al., 2023). A preliminary analysis

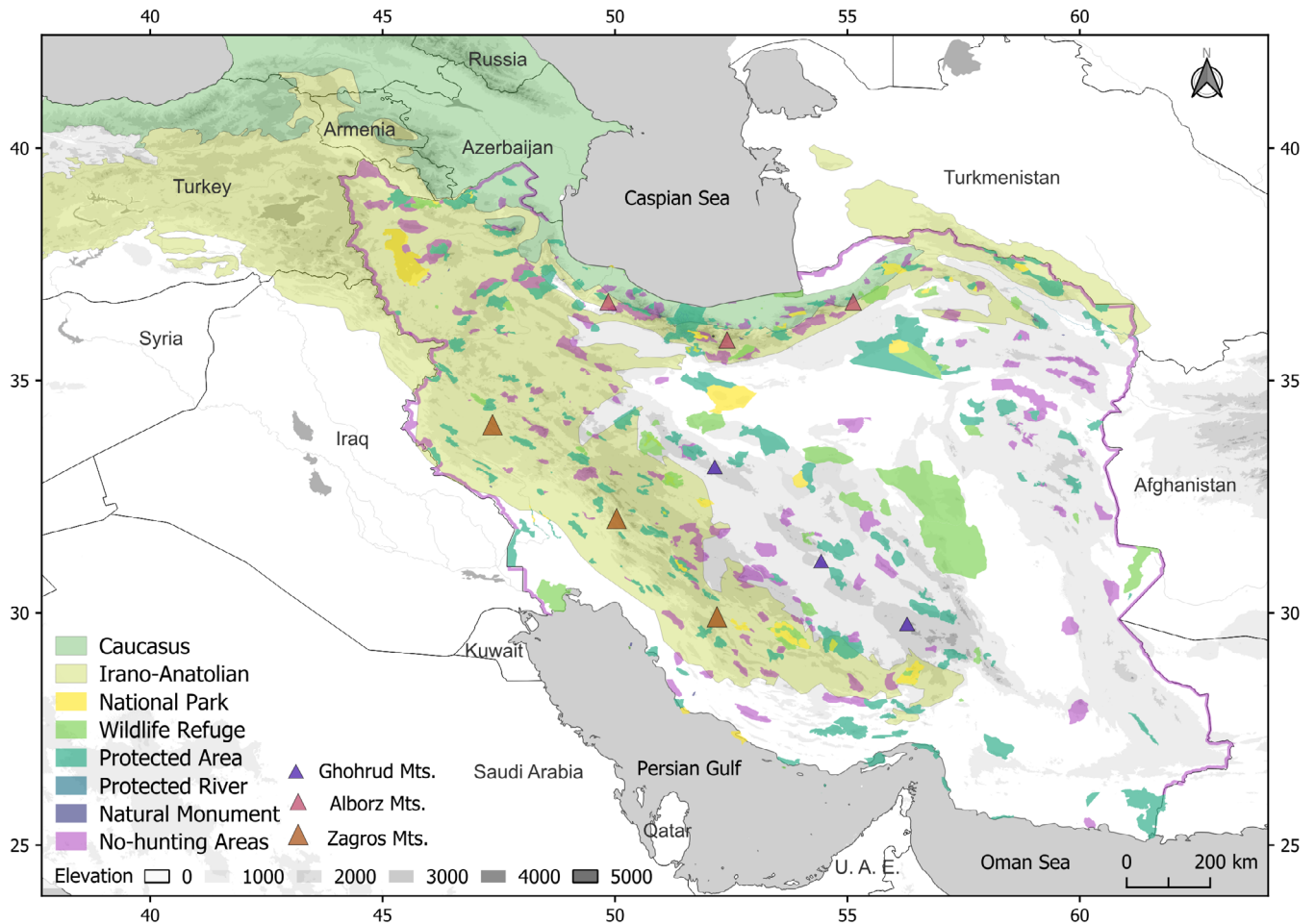


FIGURE 1 The map shows the location of Iran in the southwest Asia, with extension of two global biodiversity hotspots in the north and west: Caucasus and Irano-Anatolian across two main mountain ranges Zagros and Alborz. The map indicates the distribution of different conservation areas (CAs) and no-hunting areas (NHAs) across the country.

TABLE 1 The structure of our occurrence dataset for selected families of Iranian Lepidoptera.

Superfamily	Family	Occurrences		Endemism	
		Number of species	Occurrences	Number of species	Occurrences
Rhopalocera	Lycaenidae	209	8587	60 (29%)	1225
	Nymphalidae	139	8159	14 (10%)	305
	Pieridae	53	4380	5 (9.4%)	165
	Hesperiidae	41	1431	0	0
	Papilionidae	11	1009	2 (18%)	103
Macroheterocera	Noctuidae	960	9379	156 (16%)	854
	Geometridae	515	5279	110 (21%)	984
	Lasiocampidae	39	903	6 (15%)	128
	Drepanidae	7	258	0	0
Total	9	1974	39,385	353 (18%)	3728

of the group's diversity, in line with previous studies, indicates that the areas with a high richness of the Lepidoptera species are mainly along the Zagros and Alborz Mountains (Rajaei, Noori, et al., 2023). However, there are no systematic studies to assess the effectiveness

of the PAs in protecting areas with high rates of species richness and endemism for the group.

The primary objective of the current study is to define biodiversity hotspots of Lepidoptera at a finer geographic scale within the

GBHs in Iran. By doing so, we aim to achieve the following three goals: (1) downscaling GBHs to detect biodiversity hotspots for endemic species of Iranian Lepidoptera; (2) delineating the areas with higher priority for conserving endemic species using different biodiversity indexes for all endemic species and endemic species with extremely narrow distributions; (3) assessing the mismatch between the network of the PAs and identified species-diverse regions of the Lepidoptera to investigate the effectiveness of PAs.

MATERIALS AND METHODS

Study area

Globally, Iran is the 18th largest country by land mass extending across southwest Asia between 44–64° east and 25–40° north and covering an area of 1,648,195 km², bordering Armenia, Azerbaijan, Turkmenistan in the North, Iraq and Turkey in the West, Kuwait, Saudi Arabia, Bahrain, Qatar, the United Arab Emirates and Oman in the South and Afghanistan and Pakistan in the East (Figure 1). The heterogeneous topology of the terrestrial landscapes and sharp climate gradients provides a wide range of macro- and microhabitats in Iran, particularly within mountainous areas (Ghorbani, 2013; Madani, 2014). This topological heterogeneity of the country mainly originated from the collision of the Afro-Arabian and the Eurasian plate during the Miocene and specifically by uplifting of two main mountain ranges: Alborz and Zagros (Ghorbani, 2013). Although the majority of the country's territory features a semi-dry to dry and hot Mediterranean macroclimate, there are variations, such as temperate Siberian macroclimates in the north and tropical climates in the south and along the northern seashores of the Persian Gulf and Oman Sea (Djamali et al., 2011; Madani, 2014). The interaction of these antithetical macroclimates reflects a high ecological diversity within the country, from sandy deserts in the Central Basin and southeast to mixed Hyrcanian relict forests in the north (Dinerstein et al., 2017).

Occurrence dataset

In the course of the recently published Lepidoptera Iranica, the most complete inventory of all known lepidopteran species in Iran was compiled (Rajaei, Aarvik, et al., 2023; Rajaei & Karsholt, 2023). Despite the estimate of Landry et al. (2023) that around 45% of Iran's Lepidopteran fauna remains undiscovered, the fauna of Papilionoidea (~95% of all data employed in the current study) is regarded as nearly completely known. The occurrences for target species were extracted from Rajaei, Aarvik, et al. (2023), and the geographic coordinates of species records were carefully georeferenced using the software Google Earth Pro (v. 7.3.6.9345; Noori, Wanke, & Rajaei, 2023). In the present study, we focused on nine families of Lepidoptera with the greatest coverage of species occurrences in Iran. These include five families of Rhopalocera (Hesperiidae, Lycaenidae, Papilionidae, Pieridae and Nymphalidae) and four families of Macroheterocera

(Drepanidae, Geometridae, Lasiocampidae and Noctuidae). The total number of studied species, including endemic species, along with the number of records per family are listed in full detail (Table 1). In this study, we focused on the taxa at species level.

Data preparation

We endeavoured to encompass all target species in Iran in our analysis, even those with extremely narrow distribution represented by only few known occurrences. To reduce potential bias arising in sampling effort in our dataset, we preliminarily defined the species range using a mask of the *terrestrial ecosystems map* (TEM) for all the studied species. TEM is a high-resolution (250 m) map for the patches of different terrestrial ecosystems worldwide, which were generated according to the similarity of landscapes in biotic and abiotic factors, for example, climate and land coverage (Sayre et al., 2020).

To mask the TEM for each species, we used a minimum convex polygon to crop the species extent (alpha-hull) and then we kept only the pixel values of TEM, where the species occurred within a certain ecosystem. Since the number of occurrences varied between the studied species, the alpha-hull was generated using several R packages (R Core Team, 2022). For species with more than 10 occurrences, we used the *mcp* function in the *adehabitatHR* package (Calenge, 2006). Additionally, to delineate species potential ranges precisely, we applied species distribution models (SDMs) for species with more than 10 occurrences. However, we employed a different strategy for species with fewer than 10 records, which is explained below.

Delineating the potential range of species using SDMs

As already discussed, to avoid any overfitting in our models, we only used SDMs to estimate potential range for those species with a higher number of occurrences (>10 occurrences; Elith et al., 2011; Kreft & Jetz, 2010; Phillips & Dudík, 2008). We used the maximum entropy (MaxEnt) algorithm to model the potential distribution for each species in the study area with the help of abiotic factors characterizing temperature, precipitation and topology of the study area. We fit the model with six environmental variables, which were selected after testing by pairwise Pearson's correlation coefficients ($r \geq 0.75$) and PCA (principal component analysis; *ade4* package; Dray & Dufour, 2007; see: Figure S1, supplementary Information [SI]). These abiotic factors included 5 out of 19 bioclimatic variables obtained from the CHELSA dataset: bio5 (mean daily maximum air temperature of the warmest month), bio6 (mean daily minimum air temperature of the coldest month), bio7 (annual range of air temperature), bio13 (precipitation amount of the wettest month) and bio14 (precipitation amount of the driest month). The CHELSA dataset provides high-resolution bioclimatic variables at a global scale (30 arc sec (WGS84); Karger et al., 2017; for more details, see: <https://chelsa-climate.org>). We also included the topology of the area in our model. The topology

layer was obtained by applying the *terrain* function (as default values for computing slope and aspect) in the raster package on a digital map of the country's elevation layer (Global Digital Elevation Model, ver. 3; www.nasa.gov). Furthermore, we performed an additional analysis to consider potential bias of sampling effort in *MaxEnt* models. To do so, all pooled species occurrences were converted into a raster file and then a two-dimensional kernel density raster was generated using the *kde2d* function from the *MASS* R package (Venables & Ripley, 2002). The density bias layer represents bias in sampling intensities per location towards the area that has been sampled more intensively and is internally used by *MaxEnt* to extract background values with the same bias which effectively factors out the bias (Phillips et al., 2009; Scott Rinnan, 2015).

We investigated the best parametrization in *MaxEnt* algorithm for each studied species to avoid any overfitting or over-simplification in our models using an Akaike information criterion corrected for small sample size (AICc) approach (Ginal et al., 2022; Morales et al., 2017). To achieve this, the *MaxEnt* algorithm was executed 10 times for each species with various combinations of feature classes and regularization parameters following Ginal et al.'s (2022) procedure. Furthermore, we used the optimal model setting with AUC_{test} (Area under the ROC Curve) values ≥ 0.7 and lowest AICc to ensemble final potential species ranges based on random jackknife splits (80/20%) of occurrence data with 100 iterations (for details, see Ginal et al., 2022). A mask of the TEM, for the areas where species occurred (species extent), was used to project potential distribution as a proxy for environmental variables. The average 10% training omission threshold was used as presence-absence threshold across the 100 replicates. Supplementary information 1 provides the table of the accepted parametrization for each studied species. Finally, the multivariate environmental similarity surfaces (MESS) from the *dismo* package were used to evaluate potential areas outside of the training range of the models and hence the validity of potential species distributions (Elith & Leathwick, 2009). We assigned 1 to negative MESS values and 0 to positive values to provide a clearer perspective on similarity and dissimilarity between species occurrences and the climate space in the study area.

Delineating species range without SDM

On the other hand, for species with fewer than 10 occurrences, we delineated the potential species range using a buffer of TEM for species occurrences. To generate species ranges, we used the *rangeBuilder* function with a 10 km buffer area (Rabosky et al., 2016). This function delineates the species extent narrower than the *mcp* function. For species with up to three records, a buffer of 20 km without any alpha-hull polygon was used to define pixels within a TEM as potential species range. All the results were saved as a binary raster file (tif format) for presence/absence (1/0) of species within each pixel. Finally, the potential species ranges for all the studied species were concatenated in a raster file to generate a matrix for species presence/absence (PAM) in each grid cell of Iran at different

geographical resolution. PAM was used to calculate different species richness and biodiversity indexes for the species per grid cell.

Identification of biodiversity hotspots

Finding an optimum size for sampling unit (i.e., grid cells) is one of the long-lasting challenges in biodiversity analyses, since the scale of the study unit may influence the results of biodiversity analyses (Boyd et al., 2008; Chase et al., 2019). Therefore, we generated richness maps with different cell sizes which range between 0.008° and 1° ($30\text{--}3600$ arc sec in WGS84). We applied a pairwise Pearson's spatial correlation test to identify the largest cell size with the highest correlation compared to the original PAM raster. Consequently, we decided to represent the results of average cell size ($0.25^\circ = 900$ arc sec ≈ 650 km²; $r = 0.861$) and this cell size can accommodate the ecological and topological heterogeneity in the study area and reduce the potential spatial bias of sampling efforts. Furthermore, larger cells can reduce the precision of the gap analysis to assess the mismatch between the network of the PAs and the most species-diverse regions.

In this study, two biodiversity indexes were applied to have a better understanding of the distribution patterns of centres of endemism for Iranian Lepidoptera (Crisp et al., 2001; Myers et al., 2000). Centres of endemism represent a geographical region characterizes by a high concentration of endemic species (Myers et al., 2000). Here, centres of endemism refer to the units (here cells) with an outstanding co-occurrence of endemic Lepidoptera species. Two biodiversity indexes of endemic richness (ER) and range-rarity richness (RRR) were employed to find biodiversity hotspots (hereafter hotspots) for the endemic and narrowly distributed endemic species of Lepidoptera (Crisp et al., 2001; Noroozi et al., 2019; Orme et al., 2005; Xu et al., 2017). ER index indicates the hotspots of the endemic species within a cell, which was measured by the sum of endemic species per cell (Figure 2a). This method has been widely used to identify species-diverse regions (Cañadas et al., 2014; Crisp et al., 2001; Noroozi et al., 2019; Orme et al., 2005; Xu et al., 2017). However, the impact of widespread species might neglect species-diverse regions with co-occurrence of species with extremely narrow distribution (Orme et al., 2005; Xu et al., 2017). To overcome this challenge, we applied the RRR biodiversity index to consider the areas harbouring hotspots of endemic species with narrow distribution. RRR index was measured by summing up the contribution of each species via the reverse value for species range within a given cell (Crisp et al., 2001; Noroozi et al., 2019). Additionally, the area with highest species-diversity for all the studied species was mapped to compare the convergence with centres of endemism for the group within the country (Figure 2b).

To define the centres of endemism, we used a hotspot analysis using Getis-Ord G_i^* statistic (G_i^*) by defining the cells that spatially harbour the highest species richness for endemic and narrowly distributed endemic species of Iranian Lepidoptera (Getis & Ord, 1992; Ord & Getis, 1995). Using the p-values and z-score, the user can find the cells that cluster as hotspots with statistically significant values

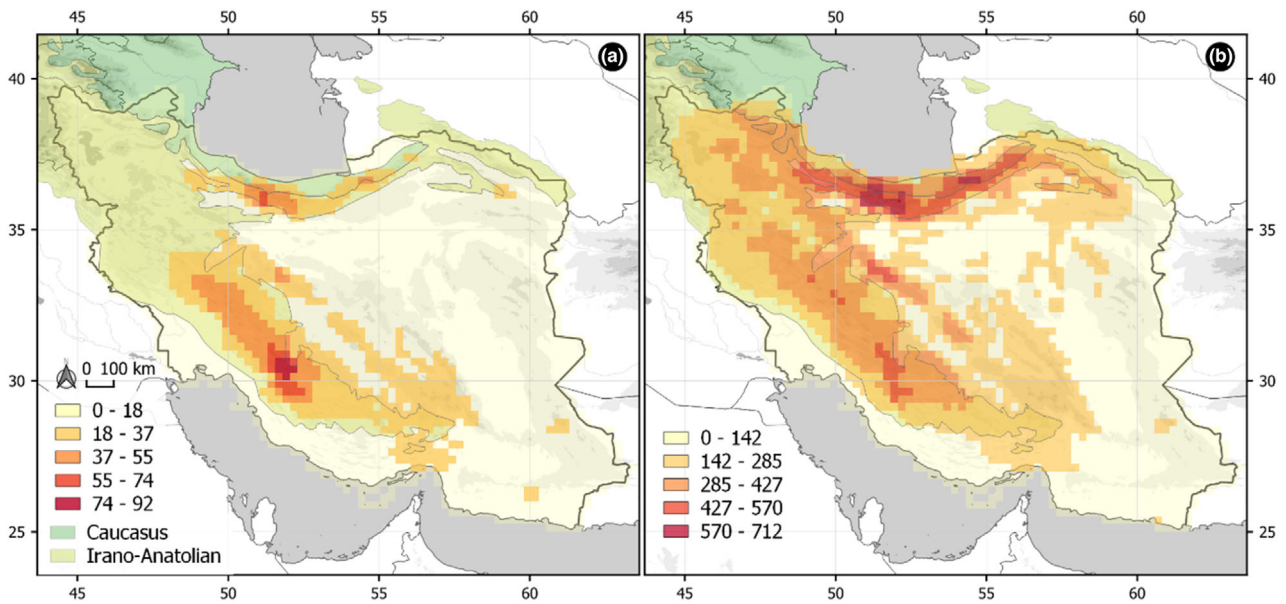


FIGURE 2 Richness of the endemic species (a) and all the studied species (b) of Lepidoptera at a resolution of 0.25° . The grey borders indicate the areas of two global biodiversity hotspots in Iran.

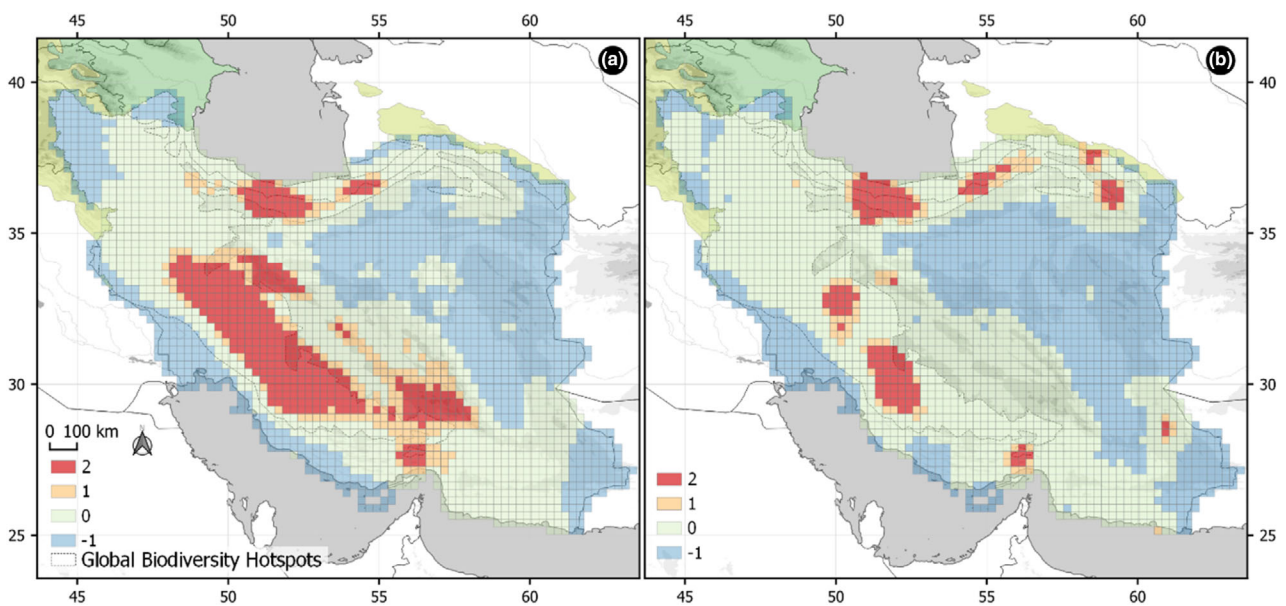


FIGURE 3 The detected biodiversity hotspots for two biodiversity indexes regarding richness of endemic species (ER; a) and range-rarity endemic species (RRR; b) of Iranian Lepidoptera. Hotspots with z-score 2 refer to cells that harbour highest richness of endemic species ($p < 0.01$), and hotspots with z-score 1 indicate cells with high richness ($p < 0.05$).

(Ord & Getis, 1995). Here we defined two levels of hotspots for cells with p -values less than <0.01 (biodiversity hotspot (hotspot-2)) and <0.05 (biodiversity hotspot (hotspot-1)) for each biodiversity index (Figure 3). These cells received z-score values 2 and 1, respectively (Getis & Ord, 1992; Ord & Getis, 1995). On the other hand, cells with insignificant statistical values have the value of zero and coldspot cells defined with z-score values of -1 , which represent the most significant lowest values of richness per cell (Noori et al., 2021; Ord & Getis, 1995).

Finally, we defined priority hotspots (PHs) by overlapping hotspots maps based on ER (Figure 3a) and RRR and summing up the hotspot's values for each cell for both indexes (Figure 3b). The PHs' maps have four levels of hotspots, representing the areas with higher priority for conservation. In the PH map, higher values represent regions harbouring both species-diverse regions of endemic and narrowly distributed endemic species (Figure 4). Respectively, PHs with the z-score of 4 (PH-4) to PH-1 represent areas with higher conservation priority for the Lepidoptera species in Iran (Figure 4). The average

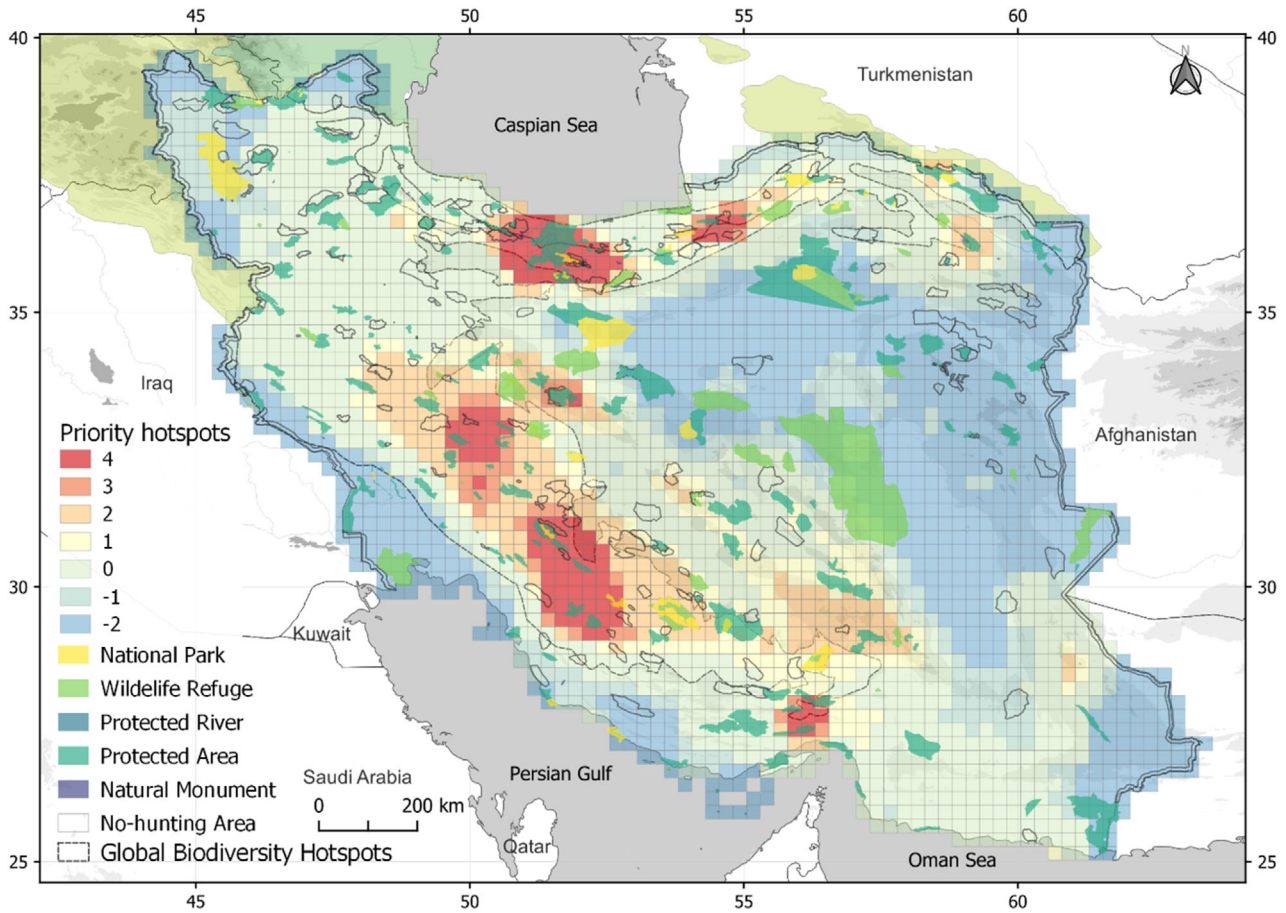


FIGURE 4 Coverage of the network of conservation areas (CAs) and no-hunting areas (NHAs) across different levels of priority hotspots (PHs) for Lepidoptera in Iran. The PHs indicated the overlapping cell with highest conservation probability for all endemic species (ER) and range-restricted species (RRR). * No-hunting areas (NHAs) have been shown transparent since they are not officially categorized as IUCN CAs in Iran.

TABLE 2 Description of all IUCN classified Iranian protected areas (PAs) in Iran, including no-hunting areas (NHAs; unclassified by the IUCN).

Design types	IUCN	Numbers	Area (km ²)	Coverage (%)		
				Iran	Irano_Anatolian*	Caucasus*
Protected Area	V	220	102951.3	6.25	6.92	9.46
No-hunting Area*	Unclassified by the IUCN	187	99087.14	6.01	8.59	10.65
Wildlife Refuge	IV	61	60529.05	3.67	1.40	1.30
Natural Monument	III	45	402.2507	0.02	0.04	0.15
National Park	II	36	20656.22	1.25	2.28	2.25
Protected River	V	16	655.3747	0.04	0.06	0.26
Covered	-	565	284281.4	17.25	19.28	24.07
Protected	-	378	185194.2	11.24	10.69	13.42

Note: The coverage column indicates the coverage percent of each IUCN category PAs and NHAs for all the country's land and the extent of two global biodiversity hotspots (*). Covered values show the sum up of the coverage for both PAs and NHAs and protected depicts only coverage of PAs. The values in bold depict the total percentage of covered and protected areas within the country and across the extent of two global biodiversity hotspots.

species richness, number of grid cells and the areas of each hotspot of ER and RRR and each PHs were assessed for further analyses (Table 3). Additionally, a non-parametric Kruskal-Wallis test was applied to assess whether detected hotspots of ER and RRR and PHs

are statistically different from each other (McKight & Najab, 2010; Figure S3). This test compares several groups of non-parametric variables (McKight & Najab, 2010). Finally, we used the *ggbetweenstats* package to explore the differences between species richness and

coverage areas of PAs and NHAs for hotspots and PHs (Patil, 2021; Figures S3 and S4).

Conservation gap analysis

We used the most updated polygon shapefiles for PAs (Iranian Department of Environment: <https://en.doe.ir/>; Figure 1). As indicated in Table 2, the PAs' dataset included spatial polygons for five different IUCN strictest categories in Iran: National Park (strictest Category II IUCN), Natural Monuments (Cat III), Wildlife Refuge (Cat IV) and PAs (Cat V; Dudley, 2008). In addition, no-hunting areas (NHAs) is an Iran-specific (unclassified by the IUCN) reserve type that has been created in the 1990s, with the aim of population recovery of threatened species. NHAs receive some levels of law enforcement by rangers (Darvishsefat, 2006; Soofi et al., 2022). The category V areas in Iran is called 'protected area' (Cat V), which might be confused with the general name of 'protected areas' used in the literature. Thus, we refer to category V areas as a replacement term for it.

To assess the extent to which PAs cover hotspots and PHs of Lepidoptera species, we conducted a gap analysis (Scott et al., 1993). In this study, we used two different definitions for the conservation gap: (i) covered, for coverage of both PAs and NHAs; and (ii) protected, for coverage of only PAs across detected hotspots and priority areas for conservation. We measured the level of spatial mismatch between the PAs and NHAs across the different levels of hotspots and PHs (Table 3). Table 3 indicates the percentage of coverage for each level of detected hotspots and PHs by established PAs and NHAs in the country. Finally, we investigated if different categories of PAs and NHAs are significantly different in covering PHs using Kruskal–Wallis test (McKight & Najab, 2010; Patil, 2021). Supplementary Information II includes a table with detailed information regarding the coverage of each established PA and NHA in conserving the PHs of Lepidoptera in Iran (Supplementary Information I (SI), section II).

RESULTS

ER versus total richness

Species-diverse regions for endemic species of Iranian Lepidoptera are mainly distributed within the two GBHs; Irano-Anatolian and Caucasus (Figures 1 and 2). These two hotspots marginally extend across the two main mountain ranges (Mountains) of Zagros and Alborz in the west and north of the country. Our results further revealed a spatial divergence between areas with higher species diversity for all Iranian Lepidoptera and endemic species in specific (Figure 2). While regions with the highest numbers of endemic species are mostly concentrated across the Zagros Mountains, the richness of all the studied species is higher along with Alborz Mountains. On the other hand, areas within the central desert basins and a narrow band in the north of the Persian Gulf and Oman Sea harbour only a small share of Lepidoptera species and endemic taxa (Figure 2).

Hotspots within hotspots

Based on our hotspot analysis for endemic species richness (ER) and range-restricted species richness (RRR), there is a substantial overlap between different levels of biodiversity hotspots (hotspots) of ER and RRR indexes. We detected six main hotspots for ER and RRR (Figure 3). While most of the hotspots are spatially convergent between the two biodiversity indexes, there are unique hotspots for the RRR index in the northeast and southeast of the country (Figure 3). Overall, most of the detected hotspots are along the main mountain ranges Zagros and Alborz and consequently fall within two GBHs. Although detected hotspots of ER and RRR cover a small proportion of the country ($\approx 21\%$ and 9% , respectively), they harbour a significant number of endemic species (8% ; Table 3).

The largest hotspot was hotspot-2 of ER, covering approximately 13.17% of the country across the highland of Zagros, Alborz and Ghohrud Mountains (Figure 3a). This hotspot consisted of cells with

TABLE 3 Areas and conservation status of Iranian Lepidoptera's biodiversity hotspots.

Hotspots	Level	Species richness (mean)	Number of cells	Area (km ²)	Iran (%)	Covered ^a (%)	Protected ^a (%)
ER	H-2	35	331	217021.88	13.17	17.88	11.19
	H-1	21	192	126382.11	7.67	18.83	14.13
RRR	H-2	39	132	85091.99	5.16	19.65	13.02
	H-1	20	93	59752.74	3.62	18.80	13.35
Priority	PH-4	45	106	68842.64	4.17	24.42	17.16
	PH-3	32	45	29319.99	1.77	15.62	10.42
	PH-2	27	222	145453.20	8.82	17.88	11.19
	PH-1	20	208	136125.62	8.25	18.83	14.13

Note: Table indicates name, species number (mean values), number of detected cells, area, proportion of the country and covered and protected areas of each hotspot. Hotspots (H) of endemic richness (ER), Rare-Ranges endemic species (RRR) and conservation priority (PHs) of Lepidoptera in Iran.

^aCovered values refer to the coverage rate of both PAs and NHAs and protected values indicate the coverage of PAs across hotspots and PHs.

the highest richness of endemic species (number of species: median = 31; maximum (max) = 92). On the other hand, although the hotspot-1 of RRR covers only 3.62% of the country, it harbours a significant number of species with restricted distribution (median = 20, max = 47; Table 3).

In line with detected hotspots for ER and RRR indexes, PHs are mainly restricted to Zagros and Alborz Mountains (Figure 4). As depicted in Figure 4, the PHs (PH-4 and 3) are mainly restricted to the central areas across the Zagros and Alborz Mountains, while two small PHs are located in the south (Geno Mountain, at the north of Bandar Abbas) and eastern Alborz Mountains (Shahkuh Mountain). The PHs-4 covers only 4.17% of the country and harbours a high rate of widespread endemic and endemic species with restricted distribution (median = 45, max = 92; Table 3). The Kruskal-Wallis test shows that different levels of PHs (PH-1 to PH-4) harbour statistically significant ($p < 0.05$) more species richness for endemic Iranian Lepidoptera, in comparison with insignificant/coldspots regions (Figure S3).

Conservation gaps

Currently, the terrestrial territory of Iran is covered by 17.25% of PAs (11.25% of all IUCN categories of PAs; 378 areas) and 'no-hunting areas' (6% of NHAs; 187 areas; Table 2). Additionally, our results indicate that PAs covered 10.69% and 13.42% of the two GBHs (Irano-Anatolian and Caucasus areas, respectively), while counting NHAs, they cover 19.28% and 24.07% of these two GBHs (Table 2). The gap analysis revealed a poor coverage of PAs and NHAs regarding both detected hotspots and PHs of Iranian Lepidoptera (mean values: protected 13% and covered 19% of the area; Figures 4 and 5; Table 3). PAs (Category V IUCN) and NHAs have the highest rate of coverage for the country's terrestrial land, 6.25% and 6.01%, respectively (Table 3; Figure 1), whereas other categories of PAs collectively cover 4.98% of the terrestrial area within the country: Wildlife Refuge (Cat. IV) with 3.67%, National park (Cat. II) 1.25%, Natural Monument (Cat. III) 0.02% and protected river (Cat. V) 0.04% (Table 3).

We found that none of the hotspots for ER and RRR indexes and PHs are protected sufficiently by PAs or covered by PAs and NHA (Table 3). PH-4 has the highest level of protection and coverage among all the other detected hotspots and PHs; however, PAs marginally protect this PHs (17.16%; Table 3). Most of the largest PAs have been established within the central desert basins and on the border with GBHs (Figure 4). On the other hand, except for Central Alborz Mountains, most of the PHs are covered and protected by small patches of PAs and NHAs (Figure 4). Finally, our result indicated that different levels of PHs for Iranian Lepidoptera are only covered by approximately 25% of the network of PAs (Figure 5). In other words, over 75% of PAs in Iran are established outside the species-diverse regions. This pattern remained unchanged when the coverage of NHAs was added to the gap analysis. The results of the Kruskal-Wallis test also indicate that the coverage of PAs and NHAs is significantly higher for non-priority areas compared with detected PHs for Lepidoptera ($p < 0.05$; Figure S4).

DISCUSSION

Hotspot within global hotspots

Lepidoptera of Iran are predominantly distributed across mountainous areas in the north and west of the country (Figure 2; Hofmann & Tremewan, 2017; Keil, 2014; Noori, Hofmann, et al., 2023; Rajaei, Aarvik, et al., 2023; Tshikolovets et al., 2014). However, there is marginal convergence between the species-diverse regions of all the studied species and our detected biodiversity hotspots and PHs for conservation (PHs) of endemic species (Figure 2). While the richness of all the species is much higher across the Alborz Mountains in the north, richness of the endemic species is more predominant in the central regions of the Zagros Mountains in the west and south (Figure 3). This might be explained by the large number of well-isolated microhabitats in central areas of the Zagros Mountains compared to the Alborz Mountains. Additionally, the entire Zagros Mountains are isolated as a large island between desert and

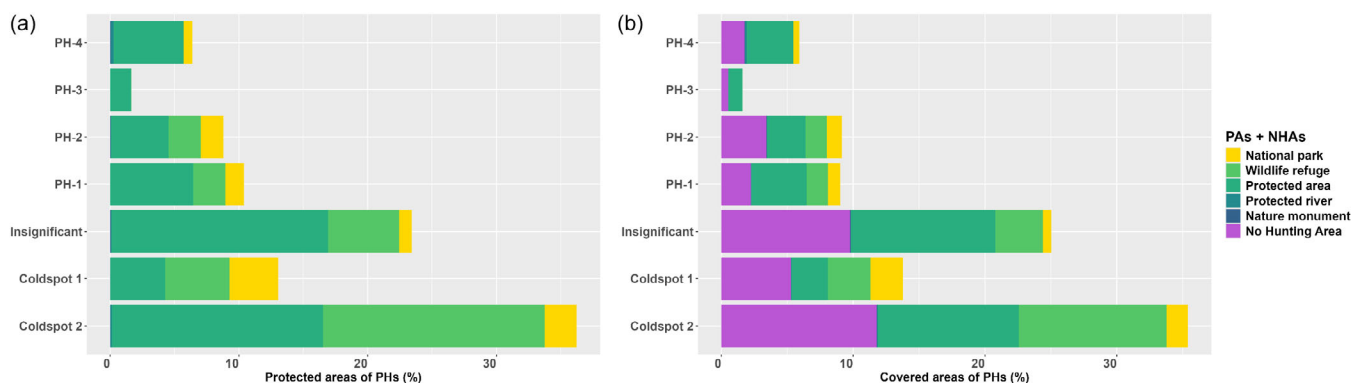


FIGURE 5 The stacked bar chart indicates the percent of protected (by PAs; a) and covered (by both PAs and NHAs; b) areas of each priority hotspots (PHs) for Iranian Lepidoptera. As shown, almost 75% of PAs and NAHs are covered in non-priority areas, and the different levels of priority areas for endemic species are roughly covered by 25% of all the network of PAs in the country.

semidesert areas inside and outside of Iran. Moreover, topological heterogeneity seems to play a central role in speciation here, as species-diverse regions, hotspots and PHs within the Zagros Mountains are extended across mountains with the highest elevations (e.g., Dena Mountain >4400 m).

Similarly, the richness of all the species and of endemic species is increasing towards the central regions of the Alborz Mountains (Figure 2). The mountains of the central Alborz regions are also of high elevation (e.g., Damavand and Alam-Kuh Mountain >4500 m). Their western and eastern flanks have faunal exchange with neighbouring regions (Hofmann & Tremewan, 2017; Werner et al., 2023), while the western parts have faunal exchange with the Caucasus, and Transcaucasia, the eastern parts share elements with the Central Asian fauna (Hofmann & Tremewan, 2017; Tshikolovets et al., 2014). Presumably, this may explain the higher co-occurrence of endemic species across the central regions of these mountain ranges. Numerous studies have independently corroborated the crucial role of mountain ranges in shaping biodiversity in Iran and southwest Asia (Ghaedi et al., 2021; Rajaei et al., 2013; Yousefi et al., 2023). As one of the main drivers of shaping the current pattern of biodiversity, mountains act as barriers and corridors for gene flow between different populations of a species and contribute to diversification (Antonelli, 2017; Perrigo et al., 2020; Rahbek et al., 2019). Higher topological heterogeneity of mountainous areas simultaneously provides centres for rapid speciation, historical refugia and regions with high rates of extinction and consequently have high evolutionary and ecological values (Harrison & Noss, 2017; Rahbek et al., 2019; Yousefi et al., 2023).

Approximately, all the detected hotspots and PHs based on Iranian Lepidoptera fall within the Irano-Anatolian and Caucasus GBHs in the north and west of the country (Figure 3). These hotspots within the global hotspots provide an excellent tool to lead conservation practices towards areas with higher genetic/evolutionary resources and ecological values (Cañadas et al., 2014; Noroozi et al., 2018). These species-diverse regions also reflect the phylogenetically diverse spots, which have been historically shaped by abiotic drivers such as geology, climate and mountains (Antonelli, 2017; Qian et al., 2023; Rahbek et al., 2019). Although detected hotspots and PHs of Iranian Lepidoptera are highly congruent and cover a small proportion of the country, they harbour a high number of endemic and non-endemic species of Lepidoptera (Figures 2 and 3). Except for the two small spots within the central desert basins and in the south of the country, all the grid cells for PH-4 and 3 fall into the two GBHs, particularly the Irano-Anatolian hotspot (Figure 4). Our results revealed that only in the Central Alborz Mountains these PHs are protected by one fourth of their areas (Figure 4). However, in the Central Zagros Mountains or eastern Alborz Mountains, PH-4 and 3 are only marginally protected by PAs or covered by PAs and NHAs (Figure 4). The areas with the highest priority (PH-4, PH-3) delineated the cells with an average co-occurrence of 45 and 32 endemic species of Lepidoptera, while they only cover 4.17% and 1.77% of the country, respectively (Table 3, Figure S3). However, these PHs have been protected only by 17% and 10% of their areas, respectively (Figure S4). In this context, a recent study by Noroozi et al. (2019) showed that 90%

of the hotspots for endemic plants are not covered by any type of PAs in Iran.

Ineffective conservation across species-diverse regions

Previous studies have raised questions about the coverage of PAs in conserving species-diverse groups in Iran, as these areas are delineated only based on vertebrates (e.g., mammals, birds, reptiles) and/or plants (Farashi & Shariati, 2017; Noori et al., 2021; Noroozi et al., 2018; Noroozi et al., 2019; Yousefi et al., 2022; Yousefi et al., 2023; Yusefi et al., 2019). In concordance with previous studies, our results revealed an extensive mismatch between the species-diverse regions of Lepidoptera and the current network of PAs (Figures 4 and 5; Table 3). The detected hotspots and PHs of Lepidoptera mainly fall within two GBHs, particularly the Irano-Anatolian hotspot (Figures 2 and 4). In general, the regions in the northern and western of Iran, across two major mountain regions of Zagros and Alborz, harbour most of the diversity for different taxa of fauna and flora (Noori et al., 2021; Noroozi et al., 2018, 2019; Yousefi et al., 2022; Yousefi et al., 2023; Yusefi et al., 2019), including Lepidoptera (Rajaei, Aarvik, et al., 2023). However, the results of the current study revealed that the network of PAs only covers 10.69% and 13.42% of the entire area for Irano-Anatolian and Caucasus GBHs, respectively (Table 2). Combining PAs with the 'no-hunting areas' (NHAs), the rate of coverage increases to 19.28% and 24.07% of the GBHs' areas (Table 2; Figure 5). Consequently, it is expected that the PAs in Iran are not able to efficiently protect the biodiversity hotspots neither at global scale nor at a finer local scale.

Misplacement of PAs in areas with lower priority for insect conservation has been already documented globally (Chowdhury et al., 2022; Venter et al., 2018). Since the 1950s, there has been a continued increase in the number and size of PAs in Iran (Jowkar et al., 2016; Kolahi et al., 2012). Currently, 378 IUCN-based PAs have been officially designed for the country (Iranian Department of Environment, 2023: www.doe.ir). The largest PAs in Iran (i.e., Lut Desert, Naybandan (Wildlife Refuge), Touran and Kavir (National Park)) have been established within the unpopulated areas of the central desert basins (Figures 4 and S2). It is probable that these PAs have been established to protect the last remaining populations of large mammals such as Asiatic cheetah (*Acinonyx jubatus venaticus*) and Persian onager (*Equus hemionus onager*). However, these areas are very distant from species-diverse regions within two GBHs in Iran (Figures 4 and S4). Hence, our result suggests the misplacement of PAs in the country towards areas with lower human–nature conflicts.

In total, the network of PAs in Iran covers only 11.24% of the land, which is far from the Aichi Target 11 for year 2020 (17%) and 2030 (30%; Butchart et al., 2015; Chandra & Idrisova, 2011; Farhadinia et al., 2022; Joppa et al., 2011; UNEP-WCMC & IUCN, 2023). On the other hand, NHAs solely cover approximately 6% ($\approx 10,000 \text{ km}^2$) of the country, which is slightly smaller than PAs (Category V IUCN) and more than sum up of all other IUCN categories

of PAs together (national park (Cat. II), nature monuments (Cat. III), wildlife refugia (Cat. IV) and protected rivers (Cat. V); Table 2). Our study indicates that some of the NHAs overlap with areas with higher conservation priority for Lepidoptera (Figure 4). Therefore, these areas can be upgraded to higher management level for conservation of hotspots and PHs of biodiversity in Iran.

PAs under anthropogenic pressure

PAs provide a bulwark to conserve biodiversity and ecosystems with higher ecological values in an effective way (Brooks et al., 2004; Pringle, 2017; Watson et al., 2014). The current network of PAs in Iran is not immune from anthropogenic effects, but not restricted to climate change (Kolahi et al., 2012). Our results showed that two GBHs in Iran extend over the most populated and arable regions in the north and west (Figure 1). The study of human footprint in Iran revealed an intensive human pressure on 22% of the PAs in the country, which is mainly distributed within the Irano-Anatolian biodiversity hotspot (Karimi & Jones, 2020). Additionally, we showed in another study (Noori, Hofmann, et al., 2023) that under pessimistic socio-economic climate scenarios, the endemic species of zygaenid moths will lose most of their habitat particularly across the central and southern regions of the country. In recent years, independent studies have issued warnings regarding extremely high temperatures and intensive droughts in the Middle East and the north of Africa in general and particularly in southern parts of Iran (Evans, 2009; Lelieveld et al., 2012; Mansouri Daneshvar et al., 2019; Vaghefi et al., 2019). Interactions of climate change with human-induced threats and conservation gaps can severely threaten species-diverse regions and centres of endemism in Iran.

Collectively, the results of this study raise questions regarding the effectiveness of the PAs for adequate protection of species-diverse areas of Lepidoptera species in Iran. Independent studies investigated the lack of effective protection of the established PAs in Iran for different groups of animal and plant taxa, yet conservation of insects in Iran has been ignored so far (Chowdhury et al., 2022; Farashi & Shariati, 2017; Noori et al., 2021; Noroozi et al., 2019; Yousefi et al., 2022; Yousefi et al., 2023; Yusefi et al., 2019). Lack of financial and human resources, mismanagement, human encroachment and lack of public awareness are among the main challenges PAs face in Iran (Jowkar et al., 2016; Kolahi et al., 2012). The results of this study indicate an obvious misplacement of PAs towards unpopulated and unfertile regions (Figure 4). Given the importance of insects in all terrestrial and aquatic ecosystems, policymakers must consider areas with higher priority for conservation in designing future PAs not only for iconic species but also less-known species of invertebrates and particularly insects (Chowdhury et al., 2022). On the other hand, the effectiveness of the established PAs should be assessed for different groups of less-studied taxa to have a better perspective of dimension and magnitude of conservation gaps in the country.

Historically, the centres of endemism have served as refugia and climatologically buffered the species during the past climate

fluctuations (Harrison & Noss, 2017). Therefore, areas with high concentrations of endemic species are considered irreplaceable regions with a high priority for conservation (Brooks et al., 2006; Shrestha et al., 2019). While our identified hotspots and PHs were delineated based on endemic species of Lepidoptera and of endemic species with highly narrow distribution, these areas extensively overlap with regions that harbour the highest species richness of all studied Lepidoptera species (Figures 2 and 4). Moreover, our identified hotspots and PHs align largely with areas prioritized for conservation of vertebrates and plants in the country (Noroozi et al., 2019; Yousefi et al., 2023). Consequently, these areas do not only concentrate conservation efforts by adding regions with higher conservation values and irreplaceability to PAs within the country but also they can strengthen the PAs to better represent the species-diverse regions of Lepidoptera. However, it is crucial to acknowledge that this study only represents an initial step in defining areas with high conservation priority for biodiversity in Iran, particularly among the mega-diverse group of invertebrates. Furthermore, investigation is warranted to delve deeper into the suggested hotspots and PHs, selecting a set of complementary sites to improve their effectiveness of PAs by encompassing biodiversity across all three levels: species, ecosystems and genetic diversity (Kati et al., 2004; Pressey et al., 1994).

CONCLUSION

Worldwide, invertebrates and especially insects were initially absent in designing different types of most PAs. To the best of our knowledge, this article represents a pioneering study that examines the conservation status of biodiversity hotspots and endemic centres of insects in Iran. We showed that the network of PAs in Iran with all its pros and cons does not well represent the species-diverse and endemic-diverse regions of Lepidoptera. Our results indicate that PAs can only marginally cover the areas of the two GBHs within the country, while these areas harbour the most species-diverse regions not only for Lepidoptera, but also for most groups of fauna and flora. Thus, conserving those identified priority areas not only benefits iconic species (i.e., Papilionoidea and Zygaenoidea) but also contributes to the protection of species from other underestimated groups of Lepidoptera, particularly micro-lepidopteran families and many potentially undiscovered taxa.

Additionally, we showed that the established network of the NHAs (unclassified by the IUCN) has the potential to be upgraded to higher ranked IUCN PA for biodiversity in Iran. Therefore, there is an immediate demand to assess the effectiveness of the currently established PAs in the country and adopt effective conservation strategies to design PAs in the areas with higher priority for conservation in the future. We also propose that upgrading or expanding the existing PAs (IUCN categories and no-hung areas) and or designing new effective PAs in the future can safeguard current biodiversity to reduce the human-induced threats and climate change.

AUTHOR CONTRIBUTIONS

Sajad Noori: Conceptualization; investigation; methodology; data curation; writing – original draft; writing – review and editing; visualization; formal analysis. **Dennis Rödder:** Methodology; formal analysis; writing – review and editing; validation; data curation; writing – original draft. **Mahmood Soofi:** Writing – review and editing. **Oliver Hawlitschek:** Writing – review and editing. **Martin Husemann:** Conceptualization; investigation; writing – review and editing; supervision. **Hossein Rajaei:** Conceptualization; investigation; supervision; writing – review and editing; data curation; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

Data S1. Supporting Information.

Supplementary Information I. A summary results of species distribution modelling using MaxEnt. The table includes the final accepted values of regularization, features, parameters, AICs, AUS and the contribution of each environmental variable in the accepted model.

Supplementary Information II. Full results of conservation status of protected areas (PAs) across hotspots of Iranian Lepidoptera. The table provides information regarding the design type of PAs, coverage and coverage score of the PAs across priority areas of Iranian Lepidoptera and species richness within each PAs.

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