DISSERTATION

"Diversity, distribution and conservation status of the Iranian Lepidoptera"

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I. **Noori, S.**, Zahiri, R., Yusefi, Gh. H., Rajabizadeh, M., Hawlitschek, O., Husemann, M. & Rajaei, H. Patterns of zoological diversity in Iran- a review. Diversity and Distribution (submitted at 17.05.2023).

II. **Noori, S.**, Wanke, D., & Rajaei, H. (2023). A gazetteer of elusive localities of Iranian Lepidoptera records. In: Rajaei, H. & Karsholt, O. (eds.): Lepidoptera Iranica. *Integrative Systematics 6 (Special Issue)*, 91-120.

III. Rajaei, H., **Noori, S.**, Karsholt, O., & Zahiri, R. (2023). General patterns of the Lepidoptera fauna of Iran. *Integrative Systematics 6 (Special Issue)*, 69-81.

IV. **Noori, S.**, Rödder, D., Yusefi, Gh. H., Hawlitschek, O., Wanke, D., Husemann, M., & Rajaei, H. Biogeographic patterns in a transition zone: a case study on Iranian Lepidoptera. Diversity and Distribution (submitted at 06.02.2024).

V. **Noori, S.**, Rödder, D., Soofi, M., Hawlitschek, O., Husemann, M., & Rajaei, H. Extensive mismatch between protected areas and biodiversity hotspots of Iranian Lepidoptera. Insect Conservation and Diversity (submitted at 01.12.2023).

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- **General introduction and discussion**

Abstract

Globally, insect populations are experiencing a significant decline primarily due to human activities. However, our understanding of the scope and severity of this decline is largely biased toward countries where biodiversity has been extensively studied. This thesis delves into the distribution patterns and conservation status of Lepidopteran species in Iran, a country at the intersection of three zoogeographical realms in southwest Asia. Within its borders lie two of the world's biodiversity hotspots. An extensive literature review was conducted on earlier studies to summarize the knowledge of zoogeographic patterns in Iran. By compiling the most comprehensive dataset of species occurrences of Lepidoptera, we delineated the species' ranges across the country. The species ranges were defined using ecosystem masking as an environmental proxy, and subsequently species distribution models (SDM). As a result, the bioregions for Lepidoptera of Iran were identified using distance-based (DM) and network-based (NM) methods. Despite some differences between the two methods, they converged on five major bioregions for the taxa across the country. These findings underscore the crucial role of the country as a potential macro-scale transitional zone, facilitating faunal exchange in southwest Asia. In line with previous studies on the fauna and flora, hotspots analysis showed that the most species-diverse regions for Lepidoptera are located across main mountain ranges in the west and center (Zagros) and north (Alborz) of the country, largely coinciding with two global biodiversity hotspots, particularly, the Irano-Anatolian hotspot. A gap analysis revealed that 75 % of the areas we defined as higher priority for Lepidoptera conservation are not protected by any IUCN categories of the existing protected areas in the country. Ultimately, by forecasting the species distribution of the Zygaenidae under different future climate scenarios, we investigated the destructive impacts of climate change on the distribution of species at the end of the current century. Our findings revealed that endemic species with narrow distributions are likely to suffer the most from these changes. Conversely, species with broader distributions may have the ability to migrate towards higher latitudes. In conclusion, the findings of the present thesis indicate Iran as an area with high diversity and endemism. The results of this thesis demonstrate that the distribution pattern of Lepidoptera in the country is not uniform, and exhibits greater complexity in southern regions, potentially serving as contact zones between zoogeographical regions. However, in line with independent studies on the impact of climate change in the Middle East, we observed that southern areas of Iran are disproportionately affected compared to northern parts of the country. Furthermore, these biodiversity-rich regions are not adequately safeguarded, due to the significant misalignment with the current network of protected areas. The information generated in this study will be useful for establishing new protected areas and upgrading the current network of protected areas within regions with higher irreplaceability and vulnerability not only for Lepidoptera but also for other groups of organisms living in the country.

Zusammenfassung

Weltweit erleben Insektenpopulationen einen signifikanten Rückgang, hauptsächlich aufgrund menschlicher Aktivitäten. Allerdings ist unser Verständnis für das Ausmaß und die Schwere dieses Rückgangs weitgehend auf Länder beschränkt, in denen ihre Biodiversität umfassend untersucht wurden. Diese Arbeit beschäftigt mit den Verbreitungsmustern und dem Erhaltungszustand der Lepidoptera-Arten im Iran, einem Land an der Schnittstelle von drei zoogeographischen Regionen in Südwestasien. Innerhalb seiner Grenzen liegen zwei der globalen Biodiversitätshotspots. Eine umfassende Literaturübersicht fasst zusammen, was über die lokalen Biodiversitätsmuster bereits bekannt ist. Durch Zusammenstellung des umfangreichsten Datensatzes zu Artenvorkommen von Schmetterlingen haben wir die Verbreitungsgebiete der Arten im ganzen Land abgegrenzt. Die Verbreitungsgebiete der Arten wurden unter Verwendung von Ökosystemmaskierung als Umweltproxy definiert und anschließend mit Species Distribution Models (SDM) und Ensemble Small Models (ESMs) bestimmt. Als Ergebnis wurden die Bioregionen für Lepidoptera im Iran mithilfe von distanzbasierten (DM) und netzwerkbasierten (NM) Methoden identifiziert. Trotz einiger Unterschiede zwischen den beiden Methoden stimmen sie in fünf hauptsächlichen Bioregionen für die Taxa im ganzen Land überein.Diese Ergebnisse unterstreichen die entscheidende Rolle des Landes als Übergangszone für den Faunenaustausch in Südwestasien. Entsprechend früheren Studien zur Fauna und Flora zeigte die Hotspot-Analyse, dass die artenreichsten Regionen für Lepidoptera entlang der westlichen Gebirgsketten im Westen, im Zentrum (Zagros) und im Norden (Alborz) des Landes liegen, die weitgehend mit zwei globalen Hotspots der Biodiversität übereinstimmen, insbesondere mit dem Irano-Anatolischen Hotspot. Eine Lückenanalyse ergab, dass 75 % der von uns als prioritär für den Schutz von Schmeterlingen identifizierten Gebiete nicht durch Kategorien der IUCN geschützt sind. Schließlich untersuchten wir durch die Vorhersage der Artenverteilung der Widderchen (Zygaenidae) unter verschiedenen zukünftigen Klimaszenarien die zerstörerischen Auswirkungen des Klimawandels auf die Verbreitung von Arten bis zum Ende dieses Jahrhunderts. Unsere Ergebnisse zeigten, dass endemische Arten mit kleinen Verbreitungsgebieten am stärksten unter diesen Veränderungen leiden werden. Dagegen könnten Arten mit größeren Verbreitungsgebieten die Fähigkeit zur Migration in Richtung höherer Breitengrade haben. Zusammenfassend stellen die Ergebnisse dieser Arbeit den Iran als ein Gebiet mit hoher Diversität und Endemismus dar. Die Ergebnisse dieser Arbeit zeigen, dass das Verbreitungsmuster der Schmetterlinge im Land nicht einheitlich ist und in südlichen Regionen eine größere Komplexität aufweist, die möglicherweise als Kontaktzonen zwischen zoogeografischen Regionen dienen. Allerdings beobachteten wir im Einklang mit unabhängigen Studien zu den Auswirkungen des Klimawandels im Nahen Osten, dass diese südlichen Gebiete im Vergleich zu den nördlichen Regionen unverhältnismäßig stark betroffen sind. Darüber hinaus sind diese biodiversitätsreichen Regionen aufgrund der erheblichen Diskrepanz zu den Schutzgebieten im Land nicht angemessen geschützt. Die in dieser Studie generierten Informationen werden nützlich sein für die Einrichtung neuer Schutzgebiete und die Verbesserung des aktuellen Netzwerks von Schutzgebieten in Regionen besonderer Bedeutung, nicht nur für Schmetterlinge, sondern auch für andere Organismengruppen, die im Land leben.

Introduction

Due to unsustainable human development, there has been a significant decline in insect diversity on a global scale. However, our understanding of the true extent and severity of this biodiversity loss is restricted to a handful of well-studied countries. Moreover, insects have been largely overlooked in the establishment of protected areas, as these regions were predominantly designed based on the distribution patterns of charismatic animals such as mammals, birds, and plants. Consequently, there is an urgent imperative to evaluate the present distribution patterns and conservation status of insects across species-diverse regions. Independent investigations have revealed a substantial impact of climate change across the Middle East, particularly in Iran. Additionally, various human-induced threats, including drought, intensified agriculture, and overgrazing, pose further challenges to biodiversity in Iran. The country hosts two global biodiversity hotspots that span major mountain ranges in its western and northern regions, serving as the epicenters of species diversity for a multitude of taxa. Nevertheless, our current knowledge of biodiversity is heavily biased towards plants and vertebrates. Consequently, a comprehensive examination of both abiotic and biotic drivers of distribution patterns is essential for gaining insights into the current state of biodiversity within the country.

Climate, topology, and geological history of Iran

As the 18th largest country in the world, Iran extends across an area of 1,684,195 km2 (roughly comparable with the combined area of the UK, Germany, France, and Spain) in southwest Asia (Fig. 1). The country has a sum of 5,440 km of terrestrial borders with Azerbaijan and Turkmenistan in the north, Turkey, and Iraq in the west, and Afghanistan and Pakistan in the east. Iran also has 2,440 km of water borders with Russia and Kazakhstan through the Caspian Sea in the north and with Kuwait, Saudi Arabia, United Arab Emirates, Qatar, Bahrain, and Oman through the Persian Gulf and Oman Sea in the south (Fig. 1; Madani, 2014).

The country is characterized by high heterogeneity in climate and topology. Most of the country is part of the Iranian Plateau, which extends across several countries in the Middle East and Central Asia (Ghorbani, 2013). The highest point of the country is Damavand Peak in the north of the country with 5,610 m above sea level (a.s.l.), and the lowest elevation is located on the seashore of the Caspian Sea at 28 m below sea level. The average elevation of the country is 1,200 m a.s.l. and approximately 17% of the land is over 2000 m (Ghorbani, 2013; Madani, 2014). The Central desert basins are surrounded by several mountain ranges (Mountains): the Alborz (Elburz) extends in the south of the Caspian Sea in the north, Zagros stretches from the northwest toward the south, Ghuhrod extends along the margin of central desert basins, Kopet-Dag in the northeast, and Makran in the southeast.

The current geological setup of the country mainly resulted from the closure of the Tethys Sea and the uplifting of mountain ranges, particularly the Zagros and Alborz by the collision of the African-Arabian and Eurasian plates (Ruban et al., 2007; Ghorbani, 2013). These mountain ranges in Iran act as a corridor and barrier for the distribution of biodiversity, not only within the country but also extending across Central Asia and the Middle East (Ghaedi et al, 2021; Yousefi et al., 2023). Additionally, independent studies revealed the crucial role of the mountain ranges in Iran as glacial refugia for different taxa during the Pleistocene glacial periods (Kehl, 2009; Ahmadzadeh et al., 2013, 2017; Paknia & Rajaei, 2015).

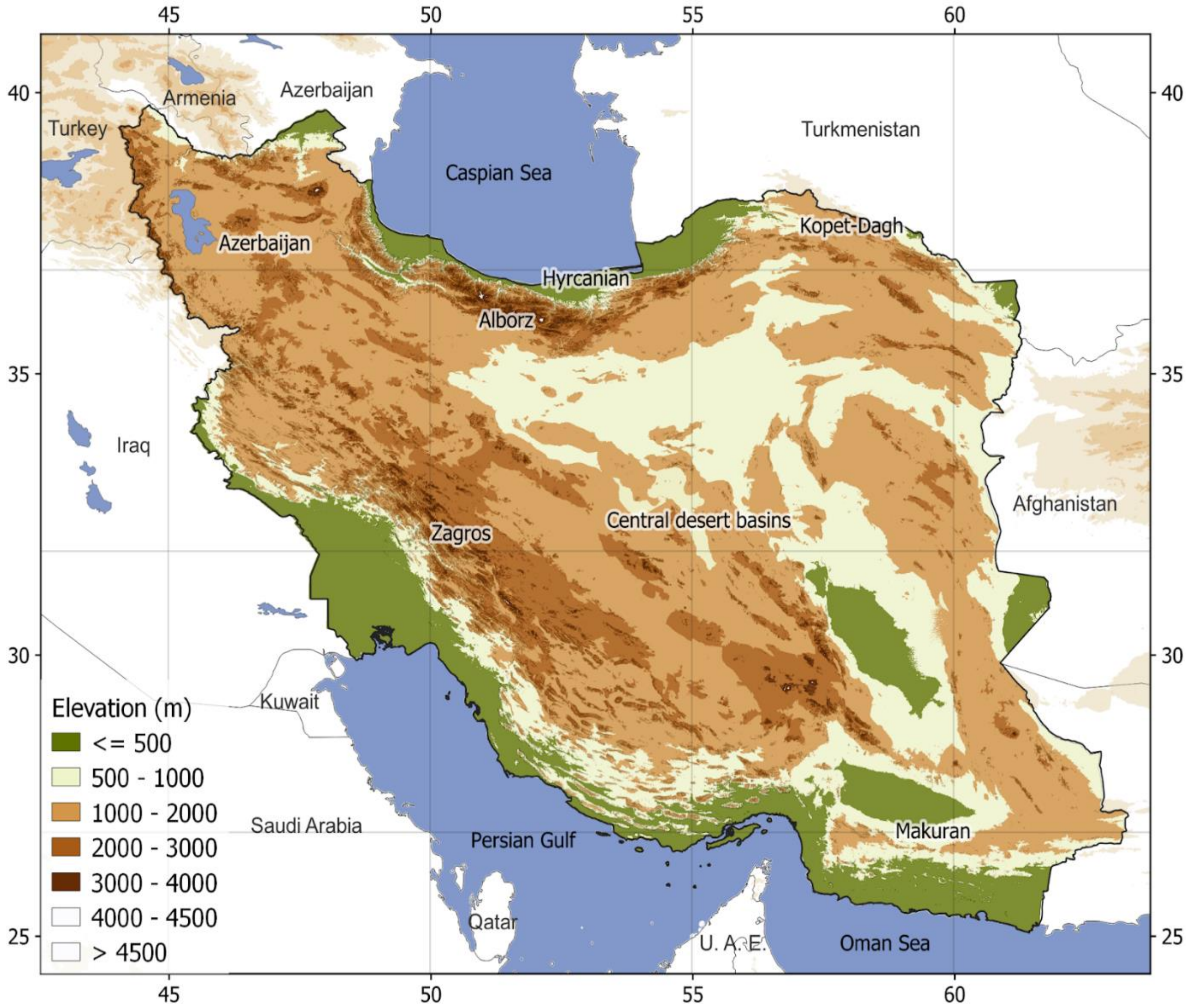

Figure 1. Geographical map of Iran. The map shows the location of the country in the southwest of Asia. The map also depicts the elevational classes and some of the major suggested regions within the country by previous studies on biodiversity.

Climatologically the country has been divided into three macroclimate regions: i. a small temperate region along with the southern coastal areas of the Caspian Sea; ii. a large mediterranean region that covers most of the country; and iii. a tropical region extending from the southwest toward the southeast of the country across the coastal areas of the Persian Gulf, and Oman Sea (Djamali et al., 2011). This setup results in a large climate variability. For instance, the lowest and highest recorded temperature was - 46 °C in the northwest and 80.83 °C in the Dasht-e Lut desert in the central deserts, respectively (Azarderakhsh et al., 2018). However, the average temperature across the country during the coldest month varies between - 6 to 21 °C and 19 to 39 °C during the hottest months (Madani, 2014).

The precipitation pattern varies steeply from 50 mm in the central deserts to above 1000 mm in the coastal areas of the Caspian Sea (with an average of 250 mm per year; Madani, 2014). Deserts cover almost 25% of the country are mainly barren and receive less than 100 mm of rainfall per year. Generally, the fertile lands are limited to the Caspian Sea coast, northwest, and west along mountainous regions, where most of the population and the largest cities are located (Statistical Center of Iran, http://www.amar.org.ir). The high heterogeneity of the topology and the steep climate gradient in Iran are reflected in the high diversity of biomes and ecoregions in the country (Dinerstein et al., 2017; Yusefi et al., 2019a). The country has been subdivided into seven biomes and 17 ecoregions (Dinerstein et al., 2017, Fig. 2a).

Biodiversity of Iran

In addition to the high diversity in the landscapes, the diversity in the flora and fauna of the country can be partly attributed to its location at the borders of three zoogeographical realms: the Palearctic, Saharo-Arabian, and Oriental (Fig. 3a; Holt et al., 2013; Ficetola et al., 2017). Furthermore, the flora belongs to three phytogeographical regions: Euro-Siberian, Irano-Turanian, and Saharo-Sindian (Fig. 3d; Zohary, 1973; White & Léonard, 1991). The majority of the Iranian fauna, particularly in the north half and western regions, belong to the Palearctic, while the fauna of the southwest and northern seashores of the Persian Gulf and Oman Sea mainly is affiliated with the Saharo-Arabian fauna (Yusefi et al. 2019a; Fig. 3a). The distribution of Oriental faunal elements is restricted to the southeast of the country (Dubatolov & Zahiri, 2005; Yusefi et al., 2019a). Similarly, the majority of the flora mainly in the central desert basins and the west belong to the Irano-Turanian, while the flora of the northern seashores of the Persian Gulf and Oman Sea is predominantly Saharo-Sindian (Fig. 3d; White & Léonard, 1991;

Zohary, 1973; Djamali et al., 2011). Euro-Siberian elements are restricted only to the narrow areas in the coastal regions in the south of the Caspian Sea (Fig. 3d; White & Léonard, 1991).

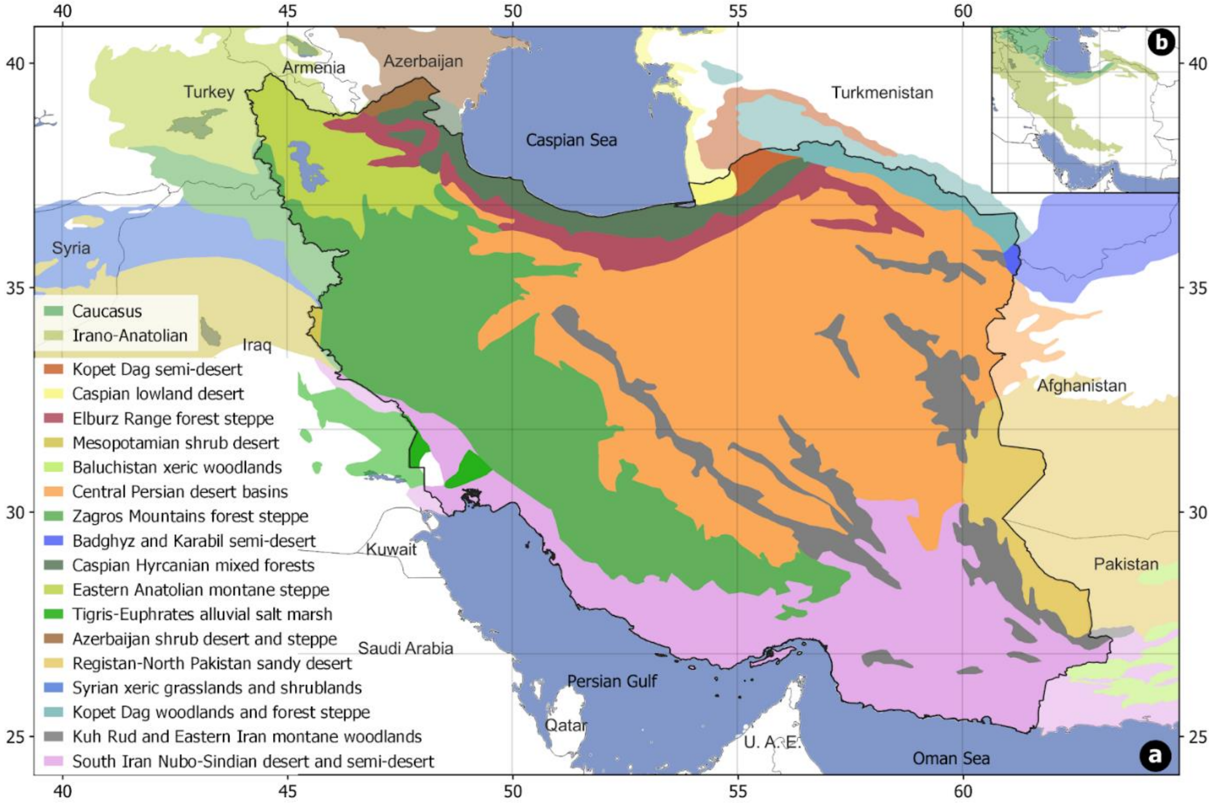

Figure 2. Ecoregions and biodiversity hotspots in Iran. a) The map depicts the extent of 17 ecoregions in Iran and the Middle East. b) The extent of two global biodiversity hotspots (Irano-Anatolian and Caucasus) in the country.

Furthermore, two of the global biodiversity hotspots mainly cover mountainous ranges in the country: the Irano-Anatolian hotspot in the northwest and west, and the Caucasus hotspot at the southern seashores of the Caspian Sea (Fig. 2b; Mittermeier, 2000; Myers et al., 2000). These two biodiversity hotspots prominently cover the major mountain ranges of the Zagros, Alborz, and Kopet-Dagh in the north and west of the country (Myers et al. 2000; Yusefi et al. 2019b; Yousefi et al., 2023).

Previous studies revealed that the regions of higher diversity of different plant and animal groups are largely restricted to the global biodiversity hotspots within the country (Noroozi et al., 2018; Rajaei et al., 2023a; Yusefi et al., 2019b; Yousefi et al., 2023). Further studies suggested that the rate of endemism for different taxa increasing toward the mid and higher elevation in the central parts of Zagros and Alborz Mountains (Noroozi et al., 2018; Yusefi et al., 2019b; Noori et al., 2021; Noori et al., 2023a; Yousefi et al., 2023). However, the species-diverse regions are not evenly distributed within the global biodiversity hotspots and different studies revealed the presence of focal hotspots within the defined biodiversity hotspots for various taxa (Noroozi et al., 2018; Yusefi et al., 2019b; Noori et al., 2021; Noori et al., 2023a). On the other hand, mountainous areas in the central desert basins, northern seashores of the Persian Gulf and Oman Sea, and the southeast harbour a high rate of species richness and endemism across various taxonomic groups (Fig. 1; Keil, 2014; Noroozi et al., 2018; Noori et al., 2021; Noori et al., 2023a).

The knowledge on biodiversity and biogeography within Iran is extensively biased toward vertebrates and plants. So far, the presence of 1,327 species of terrestrial and freshwater vertebrate taxa has been confirmed for the country, of which 13 % are endemic (Esmaeili et al., 2018; Kaboli et al., 2016; Khaleghizadeh et al., 2017; Safaei-Mahroo, 2019; Safaei-Mahroo et al., 2015; Yusefi et al., 2019 b; Yousefi et al., 2023; Çiçek et al., 2024). The flora of the country comprises 8,600 species of plants, of which 30 % are endemic (Ghahremaninejad & Nejad Falatoury, 2016; Noroozi et al., 2018 & 2019). Despite extensive long-term studies on the fauna and flora, our understanding of invertebrates remains largely fragmented (Yusefi et al., 2019a; Rajaei et al., 2023a). Several studies have been conducted across different invertebrate taxa in the last decades, but only a few charismatic groups such as crabs, butterflies, and spiders have been better cataloged (Naderloo, 2017; Zamani et al., 2022; Rajaei et al., 2023b). The knowledge regarding the other groups of invertebrates, especially mega-diverse orders of insects is limited to small checklists only for some of the families, tribes, or genera (e.g., Khayrandish et al., 2017; Enayatnia et al., 2018; Hodjat et al., 2018).

Distribution patterns of Iranian biodiversity

The biodiversity of the country has been clustered into meaningful units considering climatological and topological drivers (Fig. 1, 2a & 3). Here, a summary of the distinct and previously defined regions across the country is provided, which have been supported by independent studies for different groups of animals and plants:

Azerbaijan: This region is located in the northwestern part of the country on the border with Turkey and Azerbaijan in the southern Caucasus (Fig. 1). This region mainly covers the three provinces Azerbaijan-e Gharbi, Azerbaijan-e Sharghi, and Ardabil. The Eastern Anatolian montane steppe is the main ecoregion in this area (Fig. 2a; Dinerstein et al., 2017). Two other ecoregions of Azerbaijan are the shrub desert and steppe, and Elburz (Alborz) range forest steppe partially extends in this region (Dinerstein et al., 2017).

From the west on the border with Turkey, Azerbaijan region is separated by a high-elevation mountain range from the Anatolian region (Fig. 1). Two segregated high-elevation mountains of Sahand, Sabalan, and the Urmia Salt Lake are located within this region. The region mainly belongs to the Mediterranean desertic continental bioclimatic region with a cold and arid climate (see Fig. 1 & 3b; Kottek et al., 2006; Djamali et al., 2011). The region is bordered by the Hyrcanian region in the southern seashore of the Caspian Sea in the east and the Zagros area in the south (Fig. 2a; Dinerstein et al., 2017). The flora of this region belongs to the Irano-Turanian region (Fig. 3d; Zohary, 1973; White & Léonard, 1991).

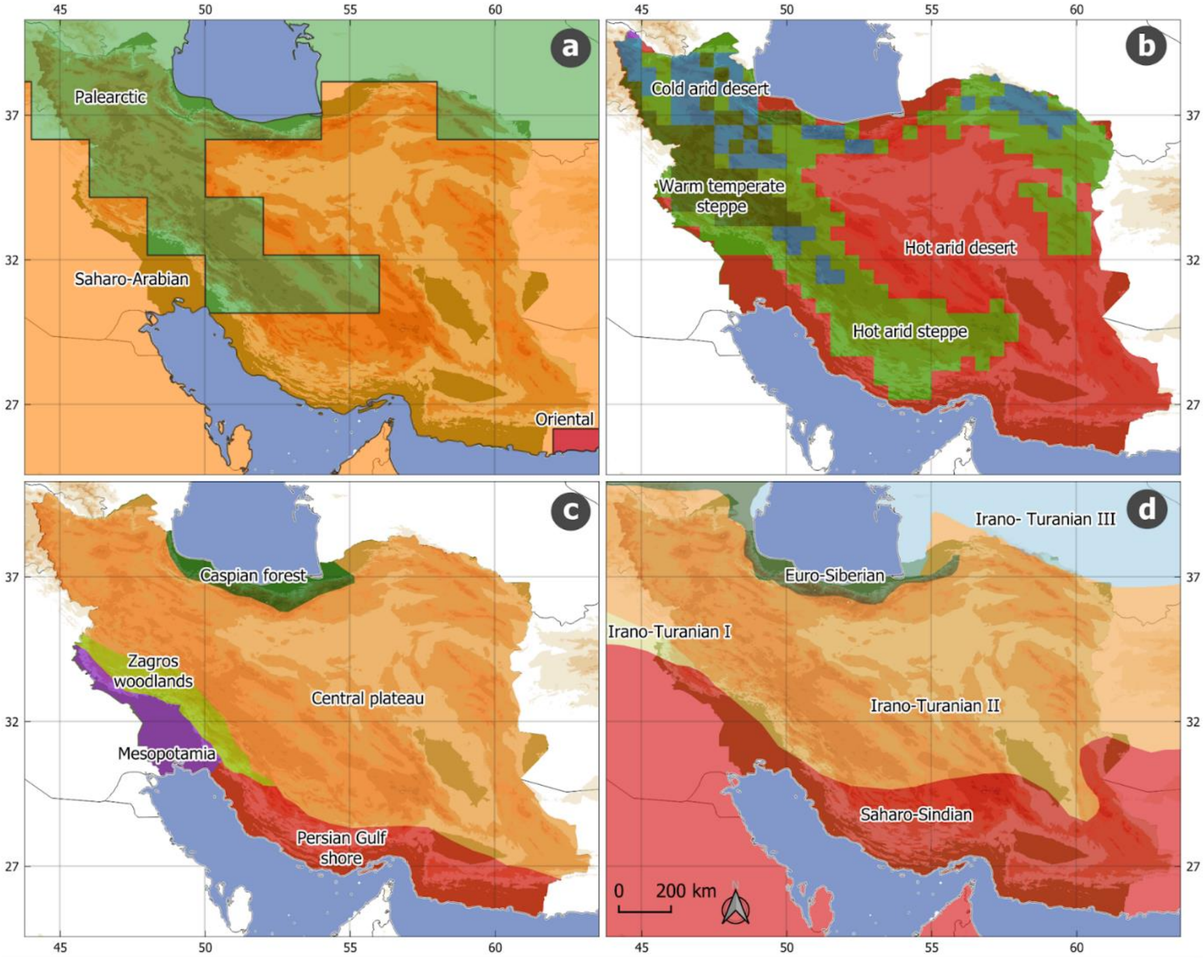

Figure 3. Zonation of Iran. a) based on zoogeographical realms (Holt et al. 2013); b) based on climate class (Köppen-Geiger 1961); c) based on zoogeographical patterns (Blanford 1876); d) based on phytogeographical regions (White & Léonard 1991).

A few studies have defined this region as a distinct region for biodiversity (Anderson, 1968; Dubatolov & Zahiri, 2005). However, the region was mainly grouped with adjacent regions like the Alborz and Zagros Mountains (Dubatolov & Zahiri, 2005; Matov et al., 2008; Yusefi et al., 2019a). This region shares several elements with the Caucasus and Transcaucasus fauna (Hofmann & Tremewan, 2017). Furthermore, this region plays an important role as a refugia and center of diversification for several western Palearctic animals e.g., spongy moth (*Lymantria dispar*) and the weevil pest (*Hypera postica*) (Zahiri et al., 2019; Sanaei et al., 2016, 2021).

Hyrcanian: This region is defined as a narrow green region extending across the southern seashores of the Caspian Sea, mainly aligned with the Caspian Hyrcanian mixed forest ecoregion by Dinerstein et al. (2017; Fig. 1 & 2a). The relict Hyrcanian forest extends for approximately 900 km through the northern slope of the Alborz Mountains in the north of Iran (Fig. 3d; Zohary, 1973; White & Léonard, 1991). Indeed, the high-elevation mountains of the Alborz Mountains trap the moisture of the Caspian Sea and consequently provide a region with high precipitation and a temperate climate. The western flank of this Hyrcanian region has a warm Temperate oceanic bio climate. Toward the eastern part, the bioclimate turns to a hot arid Mediterranean xeric oceanic in the Turkmen Sahra region (Fig. 3b; Kottek et al., 2006; Djamali et al., 2011). The flora of the Hyrcanian regions predominantly comprises Euro-Siberian plant elements (Fig. 3d; Zohary, 1973; White & Léonard, 1991).

The region has been suggested as a distinct zoogeographic region and center of endemism for different taxa: mammals (Blanford, 1876; Fig. 3c), birds (Zarudny, 1911), reptiles (Anderson, 1968), fishes (Coad, 1985; Jouladeh-Roudbar et al., 2020), Lepidoptera (Dubatolov & Zahiri, 2005; Matov et al., 2008), planthoppers (Mozaffarian, 2013), and dragonflies (Schneider et al., 2018). Furthermore, the Hyrcanian region played an important role during the Pliocene glacial periods as refugia for different taxa such as the Satyrine butterfly (*Proterebia afra*), black alder (*Alnus glutinosa*), honeybee (*Apis mellifera*), the meadow grasshopper (*Chorthippus parallelus*), the domestic mouse (*Mus musculus*), and Cynipid gall wasp (*Synergus umbraculus*) (Bartonova et al., 2018; King & Ferris, 1998; Han et al., 2012; Cooper et al., 1995; Boursot et al., 1993; Bihari et al., 2011)

Alborz: This region is one of the largest mountain ranges in Iran with the highest elevational range in southwest Asia (Fig. 1; Ghorbani, 2013; Noroozi et al., 2020a). For approximately 950 kin m length, the Alborz Mountains separates the Hyrcanian region from the rest of the country, and at the same time connects mountains from the Caucasus and Anatolia to the high-elevation mountains of the Hindu Kush in Afghanistan and Central Asia (Fig. 1; Ghorbani, 2013; Noroozi et al., 2020a; Hofmann & Tremewan, 2017). At the western flank, the Alborz Mountains meet the Talish Mountains and, in the east, connects with the Kopet-Dag Mountains in the northeast of the country. Here, the Alborz region mainly refers to the higher elevation regions and southern slopes of the Alborz Mountain, comparable with the Elborz (Alborz) range forest steppe (see Dinerstein et al., 2017; Fig. 2a). The elevation of the mountains in this region is decreasing toward the eastern and western flanks (Fig. 1).

The Alborz region has been suggested as a distinct zoogeographical region for different groups of taxa (Fig. 2a; Dubatolov and Zahiri, 2005; Paknia and Pfeiffer, 2011; Mozaffarian, 2013; Schneider et al., 2018). However, in other studies, the region grouped with other regions like the Zagros, and the central desert basins (Naumann,1987; Yusefil et al., 2019a). For example, Yusefi et al. (2019a) suggested a large bioregion for the mammals of Iran across three major mountain ranges the Alborz, Zagros, and Kopet-Dag.

The Alborz Mountains represent an impassable barrier between the Hyrcanian region and the central desert basins for many faunal elements. It simultaneously is located on the border between two major phytogeographical regions: the Euro-Siberian in the north and Irano-Turanian in the west and center of Iran (Fig. 3d; Zohary, 1973; White & Léonard, 1991; Noroozi et al., 2020a). Although the Alborz region mainly belongs to the hot and arid Mediterranean macroclimate, there are small patches of temperate microclimate in the central and eastern regions (Fig. 3b; Kottek et al., 2006; Djamali et al., 2011). The flora and fauna of this region show high endemism, particularly in the central part of this mountain range (Noroozi et al., 2020a; Noori et al., 2023). On the other hand, the Alborz Mountains act as a corridor for sharing faunistic elements among the northwest, south of the Caspian Sea, and the north-eastern regions e.g., the Persian fat dormouse (*Glis persicus*) and Caucasian pit viper (*Gloydius halys caucasicus*) (Asadi et al., 2019; Kryštufek et al., 2021).

Kopet-Dagh: The region separates the central desert basins within Iran from the central Asian regions northeast of the country (Fig. 1 & 2a; White & Léonard, 1991; Memariani, 2020). This mountain range extends on the border of the country with Turkmenistan and provides a barrier for limiting the distribution of the central Asian fauna and flora elements (Tshikolovets et al., 2014; Hofmann & Tremewan, 2017). For instance, Kopet-Dagh is located on the border between two subregions of the Irano-Turanian phytogeographical region (Fig. 3d; White & Léonard, 1991). Climatologically the region belongs to the Mediterranean microclimate, and the flora mainly represents Irano-Turanian elements (Fig. 3d; Zohary, 1973; Djamali et al., 201; Memariani, 2020). The region has been defined as a distinct zoogeographical region by several studies on reptiles (Anderson, 1968) and tiger-moth (Dubatolov & Zahiri, 2005). However, it has been mainly grouped with other regions like Zagros and Alborz (Blanford, 1876; Yusefi et al., 2019)

Central desert basins: The region predominantly embraces a large part of the Iranian plateau highland with the two largest deserts in the center of the country: Dasht-e Kavir in the north and Dasht-e Lut in the southwest (Fig. 1). Furthermore, the narrow Ghohrud Mountains (Yazd–Kerman massifs) on the eastern margin of the central desert in parallel with the Zagros Mountains feature a wide range of microclimates and harbor a high rate of endemism for different groups of fauna and flora (Mozaffarian, 2013; Keil, 2014; Noroozi et al., 2018 & 2019; Doostmohammadi et al., 2020; Noori et al. 2023). These mountains have been already mentioned as distinct zoogeographical regions by some authors (e.g. Yusefi et al., 2019; Zarudny, 1911), and have been suggested as potential refugia for some species during the glacial periods (e.g. planthoppers, Mozaffarian, 2013).

From the climatological view, most of the region has a hot and arid Mediterranean desertic regime (Fig. 3b; Kottek et al., 2006; Djamali. et al. 2011). Previous studies showed that with some differences the region can be considered a distinct zoogeographical region (Fig. 1, 2a, 3c; Blanford, 1876; Anderson, 1968; Dubatolov & Zahiri, 2005; Paknia & Pfeiffer, 2011; Yusefi et al., 2019a). On the other hand, phytogeographically the region belongs to the Irano-Turanian region (Fig. 3d; Zohary, 1973; White & Léonard, 1991).

Zagros: This region is the largest and widest mountain range in Iran, which extends for 1,300 km from the southeast of Turkey and north of Iraq toward the south of the country (Fig. 1; Noroozi et al., 2020b). Some peaks like Dena (4,409 m) and Zard Kuh (4,221 m) are covered with permanent glacial ice sheets (Noroozi et al. 2020b). The uplifting of Zagros Mountain during the collision of the Arabian tectonic plate with Eurasia in the Miocene extensively changed and shaped the current geological setup of the Iranian Plateau (Ghorbani, 2013). The Zagros region predominantly includes hot and arid steppes with a Mediterranean continental climate (Fig. 3b; Kottek et al., 2006; Djamali et al., 2011). The fauna of the region belongs to the Palearctic and the flora mainly has elements of the Irano-Turanian zone (Fig. 3a & c; Noroozi et al., 2020b).

Several studies show that the uplifting of the Zagros and Alborz Mountains acted as a barrier to gene flow for some taxa and, at the same time, as a corridor for the migration of others (e.g. Sanmartín, 2003; Ghaedi et al., 2021). The barrier effect between Afro-Arabia / Mesopotamia and the Iranian Central Basin was shown by different studies (e.g., Ahmadzadeh et al., 2017; Ghaedi et al., 2021; Yousefi et al., 2023). The Zagros and Ghurod Mountains draw impenetrable barriers in front of the distribution of the species from the Mesopotamian region toward the central desert basin and vice versa (Fig. 1; Yusefi et al., 2019a). This region has been frequently suggested as a distinct zoogeographical and phytogeographical region by independent studies (Fig. 3c; Blanford, 1876; Dubatolov & Zahiri, 2005) and center of endemism for different groups of plants and animals (Mozaffarian, 2013; Hofmann & Tremewan, 2017; Noori et al., 2023). Further studies suggested that the high elevation of the Zagros

Mountains represented as glacial refugia for various taxa such as the Yellow spotted geometer moths (*Gnopharmia*), spiny-tailed lizards (*Saara*), and mountain newt (*Neurergus derjugini*) (Rajaei Sh et al., 2013; Ghaedi et al., 2020; Malekoutian et al., 2020).

Persian Gulf and Oman Sea: It represents the region extending across the seashores in the south of Iran and together have been considered a distinct zoogeographical and phytogeographical region (Fig. 3 c & d; Blanford, 1876; Dubatolov & Zahiri, 2005; Zohary, 1973; White & Léonard, 1991). This region spans from the lowland of Mesopotamia in the southwest of Iran toward coastal areas in the southeast (Fig. 2a & 3c). The flora of this region mainly has Saharo-Sindian elements, and the fauna is predominantly affiliated with the Saharo-Arabian zoogeographical realm (Fig. 3a; Yusefi et al., 2019a; White & Léonard, 1991). The region mainly has a tropical macroclimate with hot and dry deserts (Fig. 3b; Kottek et al., 2006; Djamali et al., 2011). This region provides a corridor for connecting elements of different zoogeographical realms in the south of Iran (Dubatolov & Zahiri, 2005; Tshikolovets et al., 2014; Yusefi et al., 2019a).

Makran (Makuran): This mountainous region is located in the southeast of Iran and southwest of Pakistan in parallel with coastal areas in the north of the Oman Sea (Fig. 1). A few studies suggested this region as a distinct zoogeographical region (Yusefi et al., 2019a). However, it has been well supported that the fauna of the region harbors several Oriental elements e.g., the Baphomet moth (*Creatonotos gangis*), Asiatic black bear (*Ursus thibetanus*), and palm squirrel (*Funambulus pennanti*) (Dubatolov & Zahiri, 2005; Yusefi et al., 2019a). These species have their most western distribution in the southeast of Iran.

Conservation of biodiversity

The current protected areas (PAs) network with 378 areas in Iran roughly covers 11 % of the land (Fig. 4; Iranian Department of Environment, 2023: www.doe.ir; UNEP-WCMC & IUCN, 2023). In addition to the extensive gap between the current coverage and Aichi Targets for 17 % (2020) and 30 % (2030; Chandra & Idrisova, 2011; Joppa et al., 2013; Farhadinia et al., 2022), various studies revealed a large gap between the PAs and distribution of the biodiversity hotspots for different groups of plants and the vertebrate fauna (Farashi et & Shariati, 2017; Noroozi et al., 2018 & 2019; Yusefi et al., 2019b; Noori et al., 2021). A brief look at the distribution of PAs in the country shows that the largest PAs such as the Lut Desert, Naybandan, Touran, and Kavir are established within the central desert basin, while it has been well documented that most of the species-diverse regions in the country are mainly restricted to the mountainous areas in the west and north (Noroozi et al., 2019; Yusefi et al., 2019; Noori et al., 2021). As shown in Fig. 4, the current network of the PAs is not even able to cover species-diverse regions within the two biodiversity hotspots in the country.

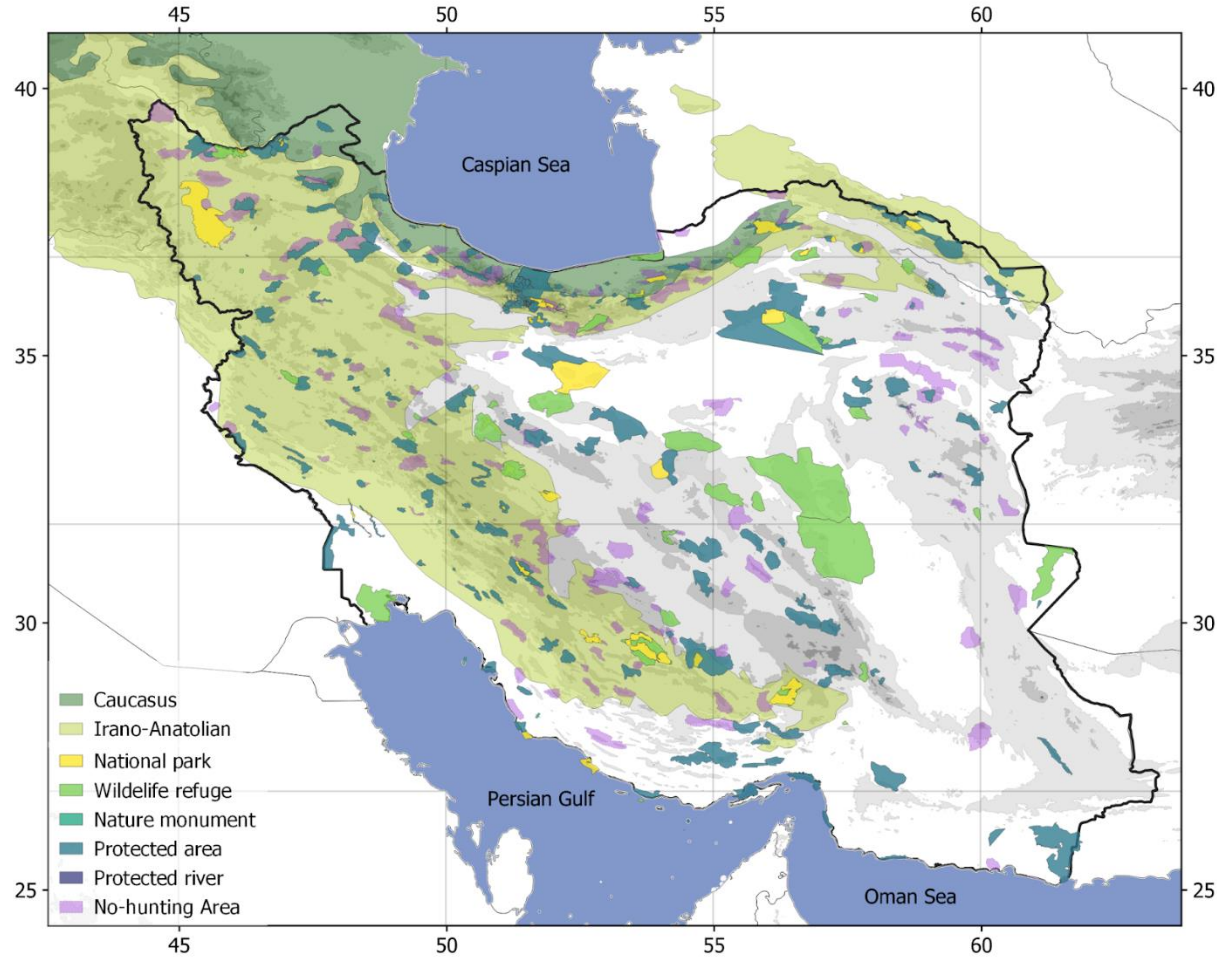

Figure 4. The network of the protected areas and no-hunting regions in Iran. The map depicts different IUCN categories for the protected areas in the country.

However, the biodiversity within the country is under high anthropogenic pressures, particularly in the north and west of the country, where the most populated regions are (Karimi & Jones, 2020). Recent studies revealed that even the areas within the current PAs are under heavy pressure from human activities (e.g., overgrazing, intensive agriculture, fire, etc.; Kolahi et al., 2012; Jowkar et al., 2016). By considering different factors for human footprint, Karimi & Jones (2020), showed that 22 % of the PAs, which are mainly distributed within the biodiversity hotspots, are under intensive human pressure.

Recently, several studies forecasted higher temperatures and deteriorating drought for countries in the Middle East and North Africa (Evans, 2009; Lelieveld et al., 2012; Mansouri Daneshvar et al., 2019). The southern regions of Iran will be affected by climate change more intensively than the northern latitudes

(Jowkar et al. 2016; Noori et al., 2023). However, these regions harbour the most complex patterns of biodiversity in the country (Yusefi et al., 2019a; Yousefi et al., 2023).

Currently, our knowledge regarding the patterns of biodiversity and related conservation studies is mainly restricted to vertebrates and plants (Noroozi et al., 2019; Yusefi et al., 2019a; Yousefi et al., 2023). There are no comprehensive studies regarding invertebrates, particularly mega-diverse groups such as insects (Noori et al., 2023; Rajaei et al., 2023a). Given this situation, there is an urgent need to analyze the distribution patterns of the less-studied groups, particularly in the southern region of the country. This would help to define the species-diverse regions for invertebrates and investigate the effectiveness of the current PAs in protecting invertebrates within the country.

Lepidoptera of Iran

Order Lepidoptera is one of the well-studied and species-rich groups of insects in the world, and likewise in Iran (Rajaei & Karsholt, 2023; Rajaei et al., 2023a & b). From the first description of *Zygaena cuvieri* by the French entomologist Guillaume-Antonie Oliver in 1796, the fauna of Lepidoptera in Iran has been documented mostly by European and Western lepidopterologists during the last two decades (Rajaei et al., 2023c). More than 1700 studies from over 900 specialists have investigated the fauna of Iranian Lepidoptera since the 18th century (Rajaei et al. 2023c). From the first early checklist of Barou (1967) to the most recent catalogue by Rajaei et al. (2023b), the documentation of the Lepidoptera fauna has been gradually compiled and completed. Researchers have published several checklists for all or part of the Lepidoptera taxa in the country (e.g., Mirzayans & Abai,1974; Nazari, 2003; Alipanah et al., 2021).

Chronologically, the major checklists include Barou (1967), Mirzayans & Abai (1974; oak-feeding species), Hashemi-Tafreshi (1970; butterflies of Tabriz city) Eckweiler & Hofmann (1980; Papilionoidea); Kallies & Špatenka (2003, 2004; Sessidae), Nazari (2003; Papilionoidea), Zolotuhuhin & Zahiri (2008; Lasiocampidae), Naderi (2012, 2019; Papilionoidea), Keil (2014; Zygaenidae), Tshikolovets et al. (2014; Papilionoidea); Koçak & Kemal (2014; all the known taxa), and Alipanah et al. (2021; Cossidae).

Through the recent project of *Lepidoptera Iraniaca*, Rajaei et al. 2023a confirmed the presence of 4,812 species from 70 families of Lepidoptera in the country. This work is considered the most updated and comprehensive catalogue of the known species of Lepidoptera in the country. From this number, approximately 19.7 % of the species are endemic, which are mainly distributed across the mountainous regions in the north and west of the country (Rajaei et al., 2023a). Even though some regions in the west and east of the country have been understudied, the preliminary results depict a higher species richness in provinces in the north (Mazandaran, Alborz, and Tehran), south (Fars) and southeast (Sistan-o-Baluchestan; Rajaei et al. 2023a). However, our knowledge is biased toward iconic and well-studied groups such as butterflies, burnet moths, and some families of macro moths (Rajaei et al., 2023 a & b). By a comparison of the known fauna of Lepidoptera in Iran and the fauna of Europe and the world, Laundry et al. (2023), revealed that probably close to 50 % of the species are still waiting to be investigated, particularly for microlepidopteran families like Gelechioidea, Tortricidae, Tineoidea, etc.

One of the main results of the project “Lepidoptera Iranica” was the most comprehensive dataset regarding the distribution of the species in Iran from more than 2,000 published references, unpublished data from different museum collections, and data obtained from personal communications. This dataset was an excellent starting point and source to study the distribution patterns of this diverse and species-rich insect group in Iran as an excellent surrogate and key indicator of the mega-diverse group of insects. The latter topic is the major target of the present doctoral thesis.

Aims

Considering the dramatic decline in insect populations worldwide and the destructive role of human activities, in this thesis the occurrence data of Lepidoptera, as an insect model group, was used to investigate the distribution patterns of biodiversity and conservation within Iran. Therefore, based on the compiled data for Iranian Lepidoptera through the “Lepidoptera Iranica” project, the following five objectives were defined to address questions regarding the distribution patterns and conservation status of different Lepidoptera species in Iran:

- Reviewing earlier studies on the distribution patterns of the biodiversity within the country to determine the gaps in our knowledge (Chapter I).
- Compiling and generating the most comprehensive occurrence dataset with high resolution for different species of Lepidoptera in Iran (Chapter II & III).
- Defining the biological regions of the Lepidoptera species of the selected families within the country and across the regions in the southwest of Asia using different bioregionalization methods (Chapter IV).
- Investigating the distribution pattern of the species diverse regions and endemic centers for selected families of Lepidoptera in Iran and assessing the coverage of the current network of the protected areas across the biodiversity hotspots (Chapter V).
- Forecasting the impact of climate change on the distribution patterns of the generalist and specialist Lepidoptera taxa by the end of the current century (Chapter VI).

Methodological aspects

Occurrence dataset

The dataset used here was compiled with data from already published references (Nazari, 2003; Tshikolovets et al., 2014; Rajaei et al., 2023b) as well as unpublished records, which were received from many Lepidopterists, who were involved in the "Lepidoptera Iranica" project (Rajaei & Karsholt, 2023). The main dataset includes all the available information for each record including taxonomic data, collection date, geographic information of the sampling sites, name of collector(s), etc. This dataset was updated and revised by the authors of the project "Lepidoptera Iranica" to assign all the records to groups according to the current state taxonomy. Less than 5 % of the records had GPS data for the longitude and latitude, however, for most of the records there was only locality data available. Those locations that were not precise enough to be georeferenced were excluded from the database (e.g., the localities with only the name of a city, or a mountain, etc.). After cleaning and taxonomically updating the dataset, all records were carefully georeferenced using the software Google Earth Pro (v. 7.3.6.9345). The final dataset comprises 58,630 occurrences data for 70 families, 1,320 genera, and 4,626 species of Lepidoptera fauna in Iran (Table 1). In the occurrence dataset, we only considered the taxa at the species level, and the subspecies occurrences were aggregated under a species name (Table 1).

Defining the species range

To reduce the potential bias in the sampling effort, we delimited species ranges using different strategies based on the available number of occurrences data for each species (Chapter IV & V). Since the number of occurrences can impact the results of the species distribution models, initially we divided the species into two groups: *group-1* including those species with less than 20 occurrences; and *group-2* including species with more than 20 occurrences.

To achieve the potential species range, first, a minimum convex polygon was generated based on the occurrences of each species within the study area. This polygon was used to crop the *terrestrial ecosystems map* (TEM) with 250 m resolution. This is a high-resolution map of all the terrestrial ecosystems worldwide (Sayre et al., 2020). TEM was generated based on the similarity between biotic and abiotic factors across different landscapes. We only accept those pixels of the TEM, for which there was an occurrence for the species within a given ecosystem. Using this method, we were able to generate a potential species range through an environmental proxy. All these steps were conducted using different packages in the R programming environment (R Core Team 2022). For species in *group-*

1, we used the *rangeBuilder* R package (Rabosky et al., 2016), while for species in *group-2*, we used the *mcp* function from the *adehabitatHR* package (Calenge, 2006). A buffer of 10 km around the occurrences was used to generate the potential species range in *group-1*, while we used species distribution models (SDM) to model the species distribution for the species in *group-2*.

Table 1. The structure of the utilized dataset in this study. The table depicts the number of genera, species, endemic species, and occurrences for 70 families of Lepidoptera in Iran. The table was sorted phylogenetically.

FAMILY	Genera	Species	Endemic	Occurrences
Micropterigidae	1	2	0	2
Nepticulidae	6	32	0	59
Adelidae	2	4	0	5
Tischeriidae	2	5	0	12
Meessiidae	3	11	4	31
Psychidae	9	15	5	58
Eriocottidae	2	2	0	2
Tineidae	19	38	3	149
Bucculatricidae	2	16	1	54
Gracillariidae	17	54	4	133
Bedelliidae	1	2	0	2
Heliodinidae	1	1	0	1
Lyonetiidae	3	3	1	4
Argyresthiidae	1	6	1	7
Yponomeutidae	4	6	0	17
Ypsolophidae	2	12	3	29
Plutellidae	6	6	3	30
Glyphipterigidae	2	4	0	8
Ustyurtiidae	1	1	1	1
Douglasiidae	2	6	0	12
Choreutidae	3	6	0	21
Galacticidae	3	3	1	3
Tortricidae	60	245	30	959
Cossidae	26	81	15	1367
Sesiidae	14	58	12	505
Brachodidae	2	14	3	72
Zygaenidae	6	74	37	1164
Limacodidae	2	2	0	4
Epipyropidae	1	1	1	1
Lecithoceridae	2	3	1	9
Autostichidae	17	61	34	198

Oecophoridae	3	14	5	35
Lypusidae	1	2	0	3
Depressariidae	7	71	6	315
Cosmopterigidae	14	31	4	136
Gelechiidae	71	215	25	667
Pterolonchidae	1	1	0	1
Elachistidae	4	11	5	37
Coleophoridae	2	183	34	477
Batrachedridae	1	1	0	3
Scythrididae	2	35	7	97
Stathmopodidae	3	6	1	17
Blastobasidae	1	1	0	2
Momphidae	1	1	0	1
Alucitidae	3	12	2	45
Pterophoridae	30	93	5	1302
Carposinidae	1	3	2	5
Epermeniidae	2	7	0	21
Hesperiidae	11	41	0	1431
Papilionidae	6	11	2	1009
Pieridae	13	53	5	4380
Lycaenidae	39	209	60	8587
Nymphalidae	38	139	14	8159
Pyralidae	146	440	128	2099
Crambidae	108	315	65	4213
Cimeliidae	1	1	0	7
Drepanidae	6	7	0	258
Lasiocampidae	13	39	6	903
Brahmaeidae	2	5	1	52
Bombycidae	1	1	0	1
Saturniidae	4	5	0	44
Sphingidae	22	36	0	668
Geometridae	147	515	110	5279
Notodontidae	18	24	2	216
Erebidae	115	333	54	3634
Euteliidae	1	2	0	18
Nolidae	13	32	3	202
Noctuidae	254	962	156	9379

Modelling the species distribution

For modelling the habitat suitability of the species, we used the high-resolution environmental variables for temperature, and precipitation from the Chelsa dataset (https://chelsa-climate.org) and Global Digital Elevation Model (ver. 3; www.nasa.gov) for topology. Consequently, we selected those variables without multicollinearity issues using pairwise Pearson's correlation coefficients ($r \geq 0.75$) and PCA, (Dray & Dufour, 2007).

We used the Maximum Entropy (MaxEnt) algorithm within the Biomod2 R package (Chapter IV, V, VI). MaxEnt has been successfully applied in a wide range of studies on modeling the species distribution (Phillips & Dudík, 2008; Kreft & Jetz, 2010). To reduce the potential bias of the sampling effort, we used the bias layer based on the sampling intensities for selecting background values (Phillips et al., 2009; Scott Rinnan, 2015). The results of the modeling by MaxEnt were evaluated using the Akaike Criterion corrected for small sample size (AICc) and Area under the ROC Curve (AUCtest) to avoid overfitting or over-simplification in resulting models (Morales et al., 2017; Ginal et al., 2022). Finally, we checked the reliability of the selected models using multivariate environmental similarity surfaces (MESS) from the *dismo* package (Elith et al., 2009).

Using the above-mentioned approach, we were able to generate a potential species range for each one of the studied species as a layer of raster with information for the presence/absence of the species in the study area. Ultimately, these steps resulted in a master matrix for the presence/absence (1/0) of species across the grid cells within the study area, which was used in further analysis for detecting bioregions of Lepidoptera (chapter III) and biodiversity hotspots of the groups (chapter IV).

Bioregionalization analysis

We employed distance- and network-based methods to cluster species communities of Lepidoptera in meaningful units within Iran (Chapter IV). While the conventional distance-based method (DM) has been applied to cluster the species hierarchy in many studies (Kreft & Jetz, 2010), the network-based method (NM) has been more recently introduced and few studies used this method (Edler et al., 2017; Yusefi et al. 2019a). We hired these two methods to compare the results and have better support for the resulting bioregions in the country.

Hotspot analysis

The potential species range was used to delineate the species-diverse regions and centers of endemism for the Lepidoptera in Iran. First using the generated master matrix we generated grid cells within the study areas for all the studied species (Chapter V). Then using two common indexes for Endemic Richness (ER) and Range-Rarity Richness (RRR), the species range for endemic species and species with extremely narrow distribution were filtered (Cañadas et al., 2014; Xu et al., 2017; Noroozi et al., 2019).

Consequently, we employed hotspot analysis using Getis-Ord Gi* statistic (Gi*) on the ER and RRR within the study area to define the biodiversity hotspots of the Lepidoptera species and the areas with higher priority for conservation (Ord & Getis, 1995). Furthermore, by concatenating the resulting hotspot map for each index, we generated and suggested higher priority for the conservation of Lepidoptera species within the country. Finally, using the gap analysis method we assessed the mismatch between the biodiversity hotspot and higher priority areas of the group with the network of the protected areas within the country (Chapter IV). In this study, we assessed the gap between detected biodiversity hotspots and areas with higher priority of the species, and different IUCN categories of the protected areas within the country (Fig. 4).

Projecting the distribution to the future

Lastly, in the final chapter, we assessed the impact of climate change on the distribution of Zygaenidae as one of the best-known groups of Lepidoptera with a high endemism rate (46%) within the country (chapter VI). We investigate the impact of climate change on the species distribution of the generalist and specialist Zygaenidae and their host plants in Iran. First, we modeled the species distribution of the host plant in the present time, and we projected them to the future climate scenarios. Considering most of the Zygaenidae species have been reported in small habitats, and there are few records for species, we employed conventional species distribution models (SDM; Phillips & Dudík, 2009) for species with more than 20 occurrences and Ensemble small models (ESMs; Della Rocca et al., 2019; Broennimann et al., 2022;) for species with few occurrences. We used MaxEnt algorithm to conduct species distribution modeling for all the studied species (Phillips & Dudík, 2009). Then, we used the resulting species distribution for the host plants to model the species distribution of Zygaenidae species in the present and future climate scenarios.

Results and Discussion

The studies presented in this thesis offer a comprehensive exploration of species-rich regions, which may be used not only for conservation planning for the Lepidoptera but also for other insect groups in Iran. This contribution tried to improve our understanding of biodiversity patterns within the country (**Chapters I, III, IV, V**). In this thesis, for the first time, I conducted a wide range of analyses on the Lepidoptera of Iran, as one of the species-rich order of insects with remarkable endemism. Lepidoptera represents an excellent model group to investigate the gap in our knowledge since they have been relatively well-studied, there is a massive amount of data, and they are keystone taxa in most ecosystems and food chains. Through this thesis, the most comprehensive available dataset (with more than 58,000 occurrences) for the Lepidoptera species in Iran was generated to improve our knowledge regarding the distribution pattern of the species (**Chapters II, III, IV**) and the conservation status (chapter V) of the group in the country.

In the first chapter, the current knowledge regarding biodiversity in Iran was reviewed to define the geological and climatological drivers that historically shaped the current distribution patterns of biodiversity within the country (**Chapter I**). Through a comprehensive literature review, we provide a robust introduction to the history of the zoogeographical studies of different taxa within the country. Additionally, we highlighted the gaps in our understanding of biodiversity distribution and proposed innovative approaches to address them, especially in the face of accelerating climate change and habitat loss. This is particularly crucial for less-studied taxa such as insects.

Unlike vertebrates and some groups of plants, the available data on the distribution of invertebrates is fragmented and scarce for the Iranian fauna. Therefore, in parallel to this project, we compiled the most comprehensive occurrence dataset for all described species of Lepidoptera in Iran in the framework of another project entitled "Lepidoptera Iranica" (Rajaei & Karsholt, 2023). The resulting dataset for Iranian Lepidoptera comprises the most updated taxonomic dataset and provides information on the endemism of each species. Besides providing the most comprehensive dataset, we provide a list of elusive localities in Iran (**Chapter II**): through georeferencing of the occurrence dataset, several historical localities were detected that were mentioned in different references, but do not exist anymore on the map, or the names have been changed during the time. In this **Chapter** (**II**) a complete list of these locality names with their current name and georeferenced occurrences were provided, which can be used in future efforts for georeferencing datasets for other taxa. The occurrence dataset of Iranian Lepidoptera is also ready to be used in further studies: It has been uploaded for our studies and after publishing the articles (**Chapters IV & V**) will be publicly available. The dataset for the last chapter (**Chapter VI**) is currently available through a GitHub repository. Using this data, firstly, we explored the distribution patterns of different families of Lepidoptera and provinces within the country (**Chapter III**). This study highlighted the predominant influence of elevation gradients on species richness and endemism.

Continental drifts, climates, and mountains predominantly shape the distribution patterns of biodiversity (Antonelli, 2017; Ficetola et al., 2017). In Iran, the current geological setup largely resulted from the collision of African and Eurasian during the early Miocene (Ruban et al., 2007). This collision continued with the uplifting of the major mountain regions, Zagros and Alborz, in the west and north of the country (Okay et al., 2010; Mouthereau et al., 2012). It has been well documented that these two mountain ranges have a remarkable impact on the distribution patterns of biodiversity as barrier and corridor (Ghaedi et al., 2021; Yousefi et al., 2023). Furthermore, the mountain ranges serve as glacial refugia for different taxa during the climate fluctuations in glacial and interglacial periods in Pliocene (Ghaedi et al., 2021; Yousefi et al., 2023).

Generally, in line with previous studies on the biodiversity patterns within the country, our findings show that the most species diverse regions for the Lepidoptera species are distributed across mountainous areas in the north and west of the country (Fig. 5a; Noroozi et al., 2018; Yusefi et al., 2019a; Rajaei et al., 2023a). These areas extend along two major mountain ranges (Zagros and Alborz;

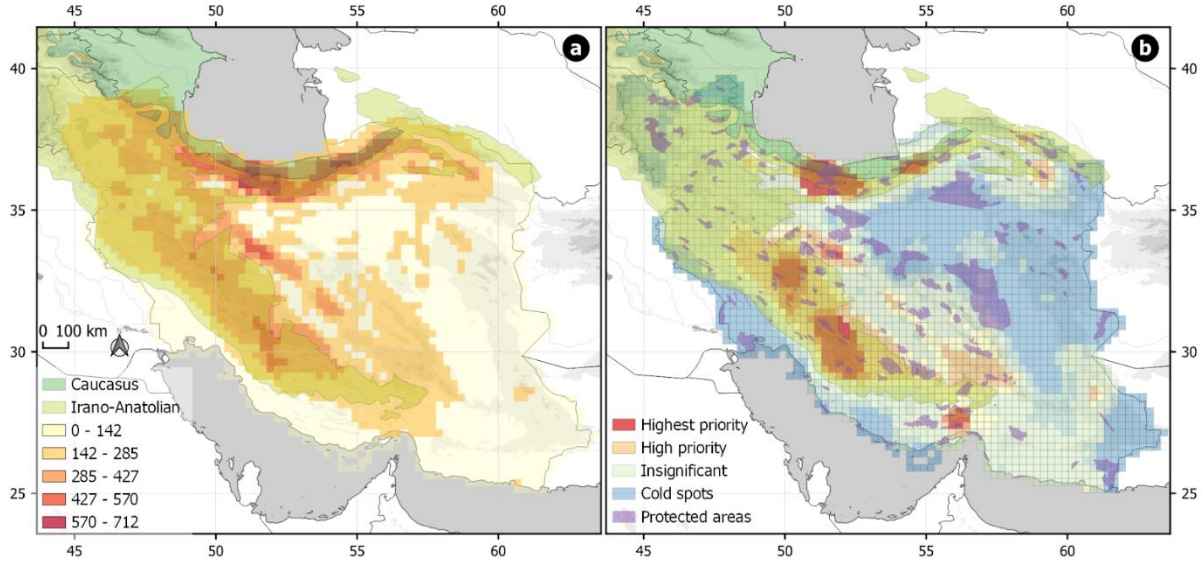

Figure 5. Distribution of species in diverse regions and areas with higher priority for conservation of Lepidoptera in Iran. a) Map of species richness of approximately 2000 species of Lepidoptera in Iran. Most of the species-diverse regions fall within two global hotspots. b) Extensive mismatch between priority areas for conservation and the network of the protected areas in the country.

Fig. 1) and the southern flanks of two biodiversity hotspots (Irano-Anatolian and Caucasus; Fig. 4). However, our findings revealed several other biodiversity hotspots in the north of the Persian Gulf and Oman Sea in the south and southeast of the country (Fig. 5b; **Chapters III, IV, V, VI**).

Biodiversity can be subdivided to meaningful regions based on the similarities and dissimilarities within species assemblage (Olson et al., 2001; Antonelli, 2017; Edler et al., 2017). The biological regions serve as experimental units for investigating the historical biotic and abiotic drivers of biodiversity distribution patterns (Antonelli, 2017; Ficetola et al., 2017). Furthermore, biogeographical units facilitate ecological, evolutionary, and conservation analysis (Olson et al., 2001; Kreft & Jetz, 2010; Bloomfield et al., 2018). In **Chapter IV** were clustered species communities of well-studied Lepidoptera families into biogeographical regions (Fig. 6). This is the first attempt to define the bioregions using distance-based and network-based methods for the insects in Iran. Formerly, Yusefi et al. (2019a), delineated different bioregions for the mammal species within the country. The other studies on the regionalization of different taxa are limited to expert opinion/descriptive approaches. Several studies conducted hierarchical analysis (Naumann, 1987; Dubatolov & Zahiri, 2005; Matov et al., 2008; Paknia & Pfeiffer, 2011; Mozaffarian, 2013), however, these studies are limited to a few taxa at the subfamily or tribe levels. We conducted bioregionalization using distance- and network-based methods, which resulted in partially convergent results (**Chapter IV**). In contrast to Yusefi et al. (2019a) in our study instead of the occurrence, we first generated a species range for each species, and thereafter the species communities were clustered to reduce the potential bias in the sampling effort and have a better image of the species distribution.

By some difference, we detected five major bioregions in the country using distance-based and network-based methods (Fig. 6; **Chapter IV**). Although there was a large convergence between the two methods, the result for network-based methods was more closely aligned with previously defined ecoregions within the country (Fig. 6). Network-based methods also detected small distinct regions that can be considered as potential transition zones between different major bioregions. As depicted in Fig. 6, two of these potential transition zones are located at the intersection of major bioregions in the southwest of the country. In **Chapter IV**, transition zones were suggested as potential contact zones between two zoogeographical realms: Palearctic and Saharo-Arabian. These regions extend across the sudden shifts in topology and climate and probably represent the transition zones. Furthermore, we discussed the role of the country as a potential macro-transition zone between distinct zoogeographical realms in southwest Asia. Due to Anthropogenic factors like habitat destruction, climate change, etc. the insect population are experiencing a dramatic decline (Hallmann et al., 2017; Wagner, 2020).

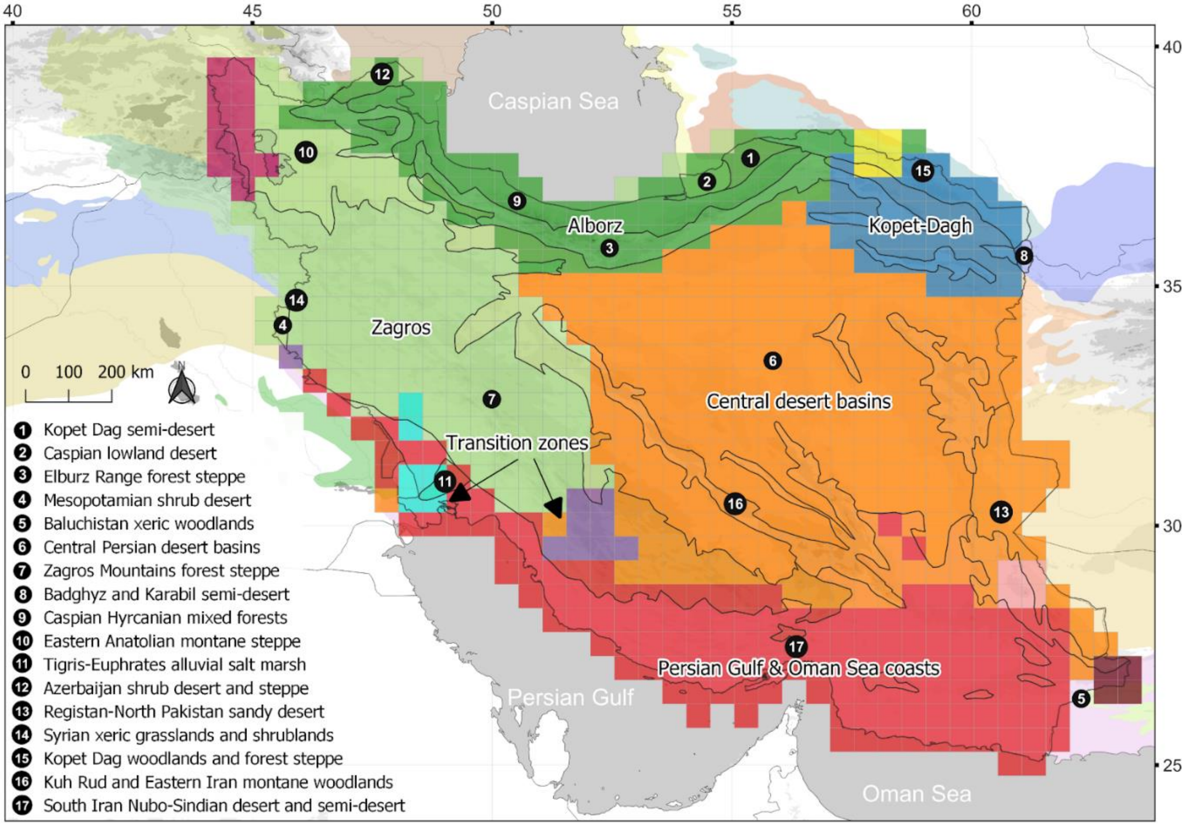

Figure 6. Bioregion map for Lepidoptera of Iran. The map depicts the predominant adaptation of detected major bioregions for Iranian Lepidoptera using network-based method and previously defined ecoregions within the country. Colors show detected bioregions and potential transition zones by network-based method.

However, our resources to protect the current biodiversity are restricted, necessitating a strategic allocation of these limited resources towards regions with higher vulnerability and irreplaceability (Pressey et al., 1994; Cañadas et al., 2014). In **Chapter V**, we delineated the biodiversity hotspots and prioritized regions for the conservation of Iranian Lepidoptera (Fig. 5b). We assessed the mismatch between these areas and the network of protected areas in Iran. Normally, vertebrates (particularly mammals) and plants are considered surrogates of biodiversity for designing protected areas (Chowdhury et al., 2022). In this study, for the first time, we used the data for an insect order in Iran to assess the effectiveness of the network of protected areas within the country. The defined biodiversity hotspots and areas with higher priority for conservation of the Lepidoptera are mainly aligned with defined hotspots for other taxa across the mountainous areas in the north and west (Noroozi et al., 2018; Yusefi et al., 2019b, Yousefi et al., 2023). Similarly, we found that the areas with higher conservation priority and species diversity of Lepidoptera mainly fall within two global biodiversity hotspots in the country (Fig. 6a; Irano-Anatolian and Caucasus). Nevertheless, our findings revealed that only 25% of the areas with higher conservation priority are covered by any IUCN categories of protected areas (Fig. 6b). We also showed that the network of the no-hunting areas (unclassified by

IUCN) in the country has a great potential to be upgraded for conserving some of the species-diverse regions. We believe the suggested areas in our study would be a useful surrogate for designing new PAs and upgrading the current network not only for Lepidoptera taxa, but also for other groups of insects and invertebrates (**Chapter V**).

Climate change has been suggested as one of the primary human-induce threats to current biodiversity (Bellard et al. 2012; Maxwell et al. 2016). However, species are to this challenge in diverse ways, employing strategies such as shifts in phenology and spatial distribution (Bellard et al. 2012; Rödder et al. 2021). Undoubtedly, are expected to impact specialist taxa more severely than generalist ones (Bellard et al. 2012; Hofmann et al. 2019). Therefore, in **Chapter VI**, we forecasted the distribution of one of the well-studied Lepidoptera taxa (Zygaenidae) and their host plants within Iran at the end of the current century to assess the impact of climate change on the distribution of the species. The Zygaenidae species are mostly mono/oligophagous, and the larvae are heavily dependent on the host plants. First, we modelled the effect of different socio-economic scenarios of climate change on the host plants of several species of Zygaenidae. Consequently, besides the other environmental variables for precipitation and temperature, we used the host plant distribution as a proxy to forecast the distribution of Zygaenidae species across optimistic and pessimistic climate scenarios. Our results revealed the deteriorating impact of climate change on the distribution pattern of the Zygaenidae species and their host plants. We found the area of habitat suitability for most species is shrinking and some species with smaller species range might even go extinct. However, while the specialist species will experience an elevational shift, generalist species will move toward higher latitudes. Our findings highlight the higher impact of climate change in the southern regions of the country. Consequently, most of the species-diverse areas of Lepidoptera, especially in the southern half of the country, are not well protected. The findings from **Chapter V** underscore the importance of prioritizing vulnerable species in the design and enhancement of Iran's existing network of protected areas.

The studies conducted in this thesis represent pioneering efforts in unraveling the distribution patterns and conservation status of one of Iran's most diverse and species-rich groups of insects These findings are poised to enhance our understanding of Lepidoptera distribution patterns within a crucial zoogeographical junction in southwest Asia. Moreover, our results establish a robust framework for future studies on Lepidoptera and insects across the country. By employing cutting-edge methodologies and utilizing the most comprehensive occurrence dataset available for Lepidoptera, we addressed several crucial questions concerning the distribution patterns and conservation status of invertebrates in Iran. Furthermore, the methodologies introduced and validated in this thesis hold promise for application to other taxa, providing deeper insights into biodiversity patterns across the country. However, the compiled occurrences dataset primarily represents well-studied families of Lepidoptera in Iran, leaving significant gaps in our knowledge regarding less-studied taxa and the fauna of neighboring countries. Closing these gaps will contribute to a more comprehensive understanding of biodiversity patterns in Iran and southwest Asia.

The outcomes of this research will provide valuable insights for stakeholders and decision-makers, guiding the allocation of limited resources towards areas of higher priority for species conservation in Iran. While, the findings of this thesis limited to better-studied families of Lepidoptera within Iran, it is evident that the areas with higher priority for conservation largely coincide with two global biodiversity hotspots. This already have been documented for other taxa such as mammals, reptiles, and plants. Therefore, future studies can identify focal biodiversity hotspots within these regions as feasible conservation targets to protect species-diverse areas. However, further studies needed to determine appropriate strategies to upgrade current network of the protected areas and design new ones that include insects and invertebrates.

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▪ Chapter I

An insight into the zoogeographical patterns in Iran

Patterns of zoological diversity in Iran – a review

Submitted in Diversity and Distribution

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Abstract

Aim. Reviewing published studies on zoogeography, we provide an overview of the biogeographic history and present patterns of Iran, highlight the gaps in our knowledge concerning zoogeographical patterns, and provide suggestions on how to close these gaps.

Location. Iran

Taxon. Animals

Methods. We reviewed publications on the distribution patterns of different groups of animal species to explore the zoogeographical regions. The historical environmental drivers were investigated to elucidate the current geological and climatological setup and consequently the distribution patterns of biodiversity. Furthermore, we highlighted the gaps in our knowledge regarding less-studied species, particularly the mega-diverse group of insects.

Results and Main conclusion. Iran represents a country with high biodiversity and complex biogeographic patterns. Its high landscape heterogeneity and steep climatic gradients result in high diversity and endemism of the fauna and flora. The current geological setup is largely a result of several processes of orogeny and plate collision during the Mesozoic and the Cenozoic, along with the development of the Tethyan Sea, but particularly the uplifting of several high mountain ranges during the Miocene. The mountains uplifting processes apparently have had a profound role in shaping the current faunal diversity patterns by acting as barrier, corridor, and glacial refugia. The country has been considered a biogeographic transition zone among three zoogeographical realms, where different faunal elements from the Palearctic, the Oriental, and the Saharo-Arabian zones collide, which emphasizes the complex biodiversity patterns. This complexity made inferring biogeographic divisions particularly difficult in the case of the local fauna, hence the number of zoological zones differs from taxon to taxon. However, our knowledge of the distribution of biodiversity in Iran is limited, even in the case of some well-studied taxa like plants, vertebrates, and a few families of the Arthropoda.

Keywords: Biogeography, Caucasus hotspot, climate oscillations, Irano-Anatolian hotspot, mountain uplift, Oriental, Palearctic.

Introduction

Iran is a large country in western Asia, its territory overlapping with two global biodiversity hotspots, the Caucasus, and the Irano-Anatolian (Fig. 1a & b; Mittermeier, 2000; Myers et al., 2000). Despite its importance for global biodiversity as a major biogeographical transition zone, where three of the world's biogeographical realms –Palearctic, Saharo-Arabian, and Oriental– overlap, the patterns of faunal diversity of the country remain poorly studied (Fig. 1a; Holt et al., 2013; Ficetola et al., 2017). But more importantly, an extensive review of the scattered literature on the topic is missing. We aim to close this gap by providing a comprehensive review of the zoogeographical patterns starting with its geological and climatic setup and then summarizing known distribution patterns of various animal groups to reveal larger-scale biogeographic paradigm.

Biogeography is the study of the distribution of species and their underlying patterns (Briggs, 1995; Hominick, 2002; Richardson & Whittaker, 2010; Cox et al. 2016). The geographic and climatic setting of a region represents the prerequisite for its biodiversity and is apparently the main determinant of biogeographic structures (Antonelli, 2017; Ficetola et al., 2017; Holt et al., 2013). Hence, to understand the biological patterns of a region it is crucial to study and review its geological and geographical settings first, together with its past and present climatic patterns.

Abiotic patterns

Geography, geology, and climate – the present

Iran (formerly Persia) is located between 44-64° east and 25-40° north and covers an area of 1,648,195 km^2 (only slightly smaller than the combined size of UK, France, Germany, and Spain). The country is surrounded by two large water bodies, the Persian Gulf and the Oman Sea to the south and the Caspian Sea to the north (Fig. 1). On land, the country is bordered by the Anatolian/Caucasian highlands of Armenia, Azerbaijan, and Turkey in the northwest and the lowlands of Kurdistan and Mesopotamia in Iraq in the west; in the northeast, the country is bordered by Turkmenistan and by Afghanistan and Pakistan in the east. Most of the current territory of Iran forms the Iranian Plateau, which is part of the Eurasian plate, situated between the Indian plate to the east and the Arabian plate to the west. This constellation is the result of the migration of northern Gondwana to southern Laurasia during the Paleozoic–Mesozoic periods (Ghorbani, 2013; Lerosey-Aubril, 2012; Lerosey-Aubril & Feist, 2012), which gave rise to a mosaic of higher and lower mountain ranges in various shapes and degrees of erosion, (Ghorbani, 2013; Ruban et al., 2007). The two largest and highest mountain ranges are the Alborz and Zagros; the Alborz (or Elburz) Mountains extend along the north end of the Iranian Plateau and its northeastern extension borders the Kopet-Dag (or Kopeh-Dagh) Mountains. The Zagros Mountains are located along the west side of the plateau with its southeastern extension bordering the Makran (or Makuran) Mountains in Baluchistan. The vast region located between these mountain ranges is known as the Central Basin, which is not a flat plain, but a region with high physiographic complexity containing several scattered large mountains and many small mountains. The elevation, with a mean of 900 m, ranges from -56 m in the hyperarid Lut desert to 5,610 m at the Damavand peak, overall declining towards the coastal regions of the Persian Gulf and the Oman Sea (Fig. 2; Ghorbani, 2013; Madani, 2014).

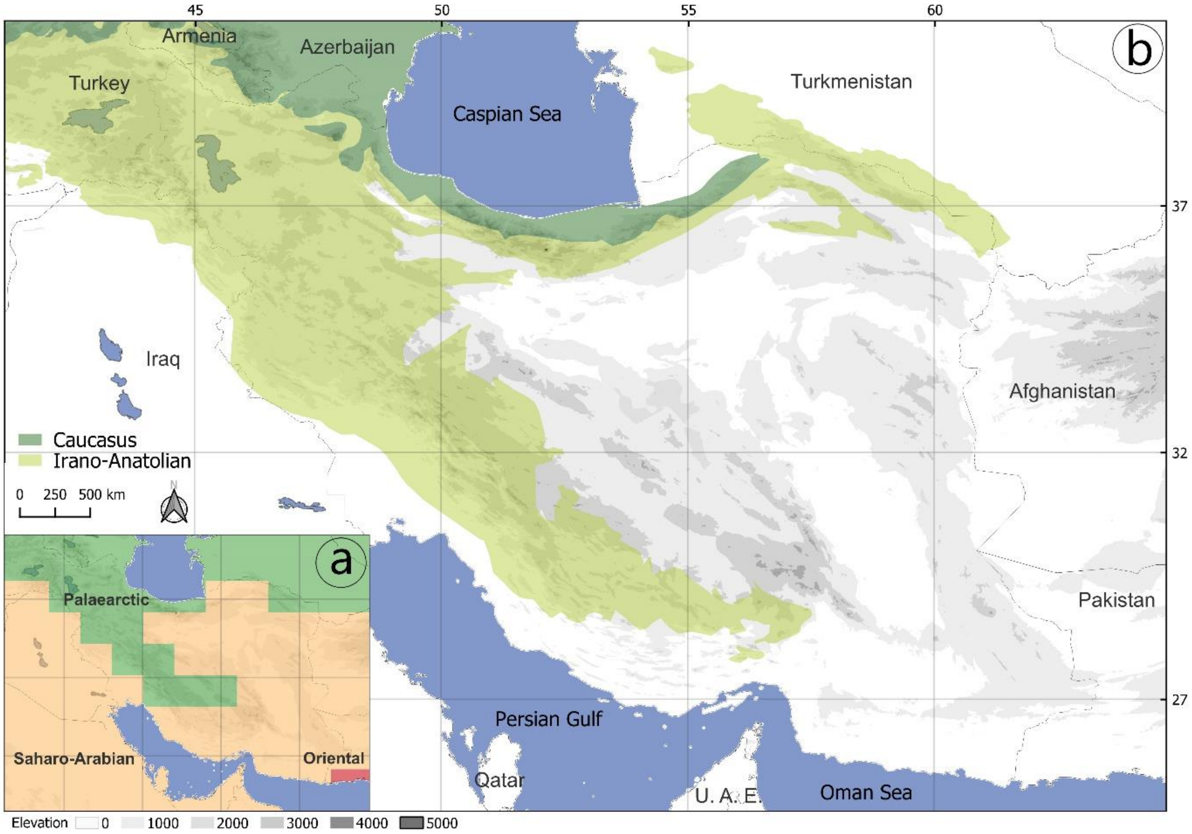

Figure 1. a) Iran intersects with three global zoogeographical realms: Palearctic, Saharo-Arabian, and Oriental. b) The western and northern regions of Iran belong to two of the global biodiversity hotspots (Caucasus and Irano-Anatolian).

The geographical complexity of Iran generates both diverse and extreme climates, including cold Siberian, temperate humid, and hot subtropical regions. The most extreme ground surface air temperatures recorded to date are −46 °C in the northwest and 80.83 °C in the Dasht-e Lut, with an average between -6 to 21°C in coldest months and 19 to 39°C in the warmest months (Fig. 2a; Madani, 2014; Azarderakhsh et al. 2018). Likewise, the annual rainfall is highly variable, ranging from less than

100 mm in some parts of the central desert basins up to above 2,000 mm in some parts of the Caspian Sea coasts (Fig. 2b; Iran Meteorological Organization, http://www.irimo.ir/eng; Fig. 2). Overall, the precipitation decreases, and temperature increases along a gradient from northwest to southeast; yet a large portion of the country is arid to semi-arid with a low mean annual precipitation (about 250 mm; Ghasemi & Khalili, 2008; Madani, 2014). Precipitation variability is largely associated with the mountains, mainly the Alborz and Zagros Mountain ranges (Mountain) in the north and west (Fig. 2c; Rahimzadeh et al., 2009), which receive higher rainfall compared with lowlands. According to Djamali et al., (2011), Iran contains three (Mediterranean, Temperate and Tropical) out of five world macro-bioclimates (Rivas-Martínez et al., 2011), including 11 of the 17 bioclimates that exist in these three macro-bioclimates. More recently, Yusefi et al., (2019a) identified eight climatic regions inside the country by using a model-based cluster analysis of 13 bioclimatic variables, mostly representing

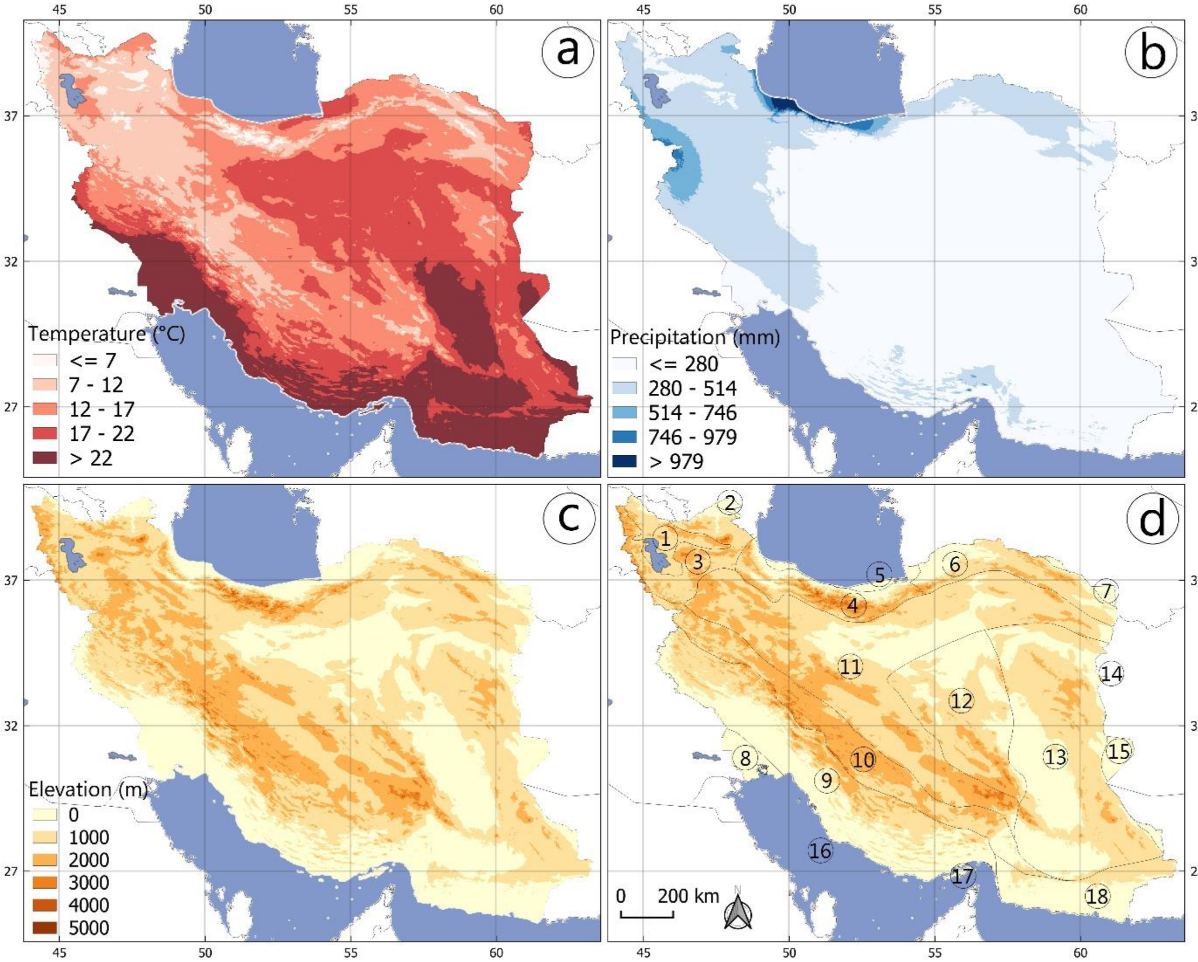

Figure 2. Maps of different abiotic variable for Iran. Maps for average, a) temperature (° C), b) precipitation (mm) in Iran between 1970 – 2000 (www.worldclim.org), c) elevation (m), d) 18 geological provinces for Iran (based on Pollastro et al., 1999) : 1) Araks, 2) Kura Basin, 3) Lesser Caucasus, 4) Alborz Fold Belt, 5) South Caspian Basin, 6) Kopet-Dag Foldbelt, 7) Amu-Darya Basin, 8) Mesopotamian Foredeep Basin, 9) Zagros Fold Belt, 10) Zagros Thrust Zone, 11) Central Iranian Basins, 12) Central Iranian Microcontinents, 13) Lut Block and Depression, 14) Central Afghanistan, 15) Baluchistan, 16) Qatar Arch, 17) Rub Al Khali Basin, 18) Makran.

temperature and precipitation, two general climatic variables (aridity index and global potential evapotranspiration), and a terrain ruggedness index. The above-mentioned high geological and climatic heterogeneity results in high habitat diversity in the country: seven of the 14 described global biome types, including 19 different ecoregions are found there (Dinerstein et al., 2017; Fig. 3), which in turn gives rise to a substantial faunal and floral diversity.

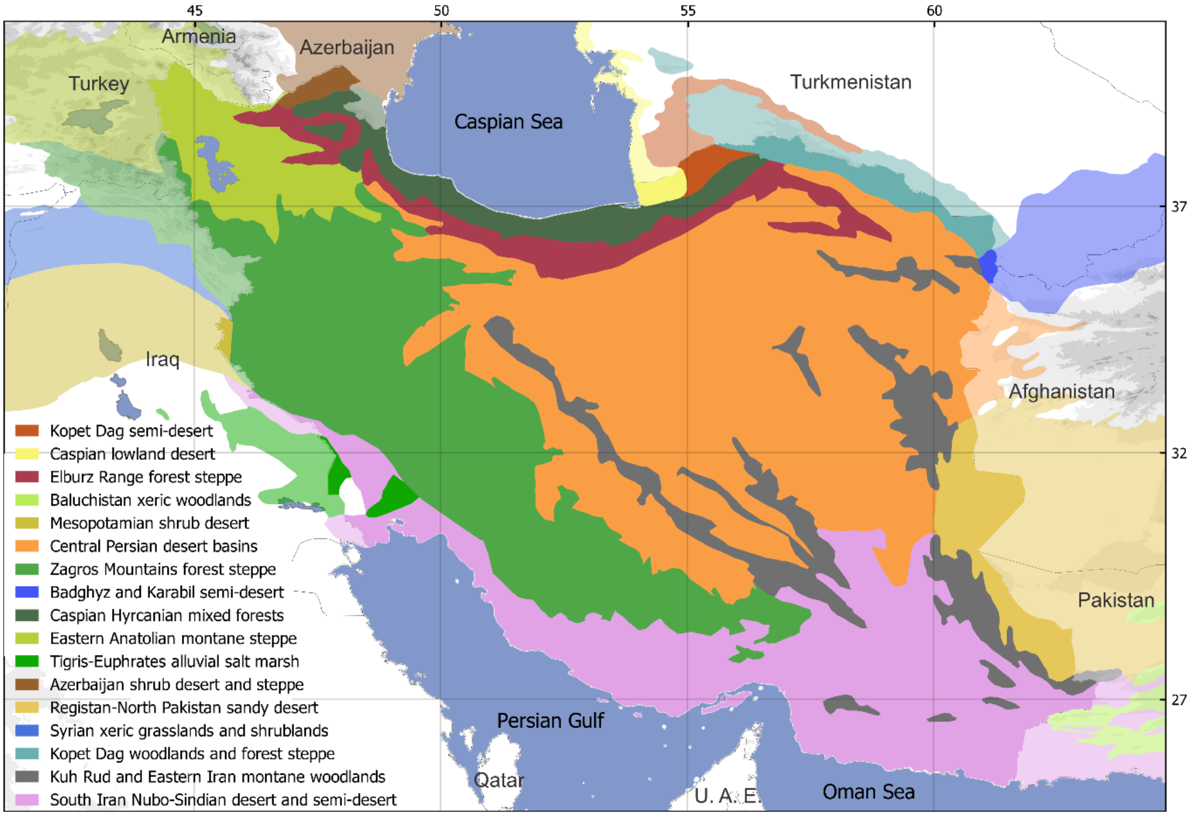

Figure 3. Diversity of ecoregions within the terrestrial territory of Iran (https://ecoregions.appspot.com/).

Geography, geology, and climate – the past

The current biodiversity of the country is, however, not only dependent on the current conditions but is largely shaped by past geological events and climatic fluctuations. The collision of the African, Arabian, Eurasian, and Indian Plates resulted in the uplift of several mountain chains in the north, west, and south of Iran (Ruban et al., 2007). Four major periods played a large role in the current setup of the country starting 4,600 million years ago (MYA) according to the literature.

I. Paleozoic, Mesozoic, and early Cenozoic. Throughout the Paleozoic (540-260 MYA), the Iranian and Arabian plates were connected to the northeastern margin of the Gondwana supercontinent, separated from Laurasia via the Proto-Tethys Ocean (Berberian & King, 1981; Stampfli & Borel, 2002). Evidence from the paleo-geographical study of the trilobite fauna of Iran and Armenia suggests a single biogeographic unit for three microplates of the region at that time: the Alborz, Central Iran, and Transcaucasia in the Middle and Late Permian (Fig. 2d; Lerosey-Aubril & Feist, 2012; Ruban et al., 2007). During the Hercynian (or Variscan) orogeny, some microplates of Iran, Afghanistan, and some other regions (Cimmerian Superterrane) separated from Gondwanaland and collided with the southern part of Laurasia during the late Triassic (230 MYA), which resulted in the primary formation of the Alborz (like a hill-shaped projection), concurrent with the closure of the Paleo-Tethys Ocean and opening of the Neo-Tethys Ocean in its wake (Ricou, 1994; Ruban et al., 2007; Stampfi & Borel, 2002). Although some authors have suggested a Laurussian affinity of the adjacent Alborz, Northwest and Central Iran terranes (Darvishzadeh, 2003; Kalvoda, 2002), others consider them as a part of the Cimmerian Superterrane which rifted from the north of Gondwana (Ruban et al., 2007; Stampfi & Borel, 2002). Later, at the border of the late Triassic to early Jurassic (210 – 195 MYA), folding and uplifts occurred on the central Iran plate through the Cimmerian orogeny that resulted in partial emergence of the Central Iranian plains from the sea, closing the Paleo-Tethys Sea (Paleozoic) and opening the Neo-Tethys Sea (Mesozoic to Cenozoic; Ghorbani, 2013; Ruban et al., 2007). The Tethyan seaway connected two major oceans during the Oligocene: the Atlantic and Pacific Ocean through the present-day Middle East and the present-day Mediterranean Sea (Harzhauser et al., 2007). These tropical lowlands were covered with forest vegetation (Darvishzadeh, 2003). At the beginning of the Paleocene epoch (65 MYA), the Tethys began to close, and the Alpine-Himalayan orogenic belt developed along the boundary of the African and Eurasian mega-plates, which also initiated the formation of the Alborz and Zagros Mountain ranges (Storetvedt, 1990).

II. Early Miocene: The Arabia–Eurasia collision. The Miocene period mainly shaped Iran through the collision of the Arabian and Eurasian plates (Berberian & King, 1981; Ruban et al., 2007). Later, in the Eocene, especially in the southeast of the country, the Indian and Eurasian plates (45 MYA) played an important role (Darvishzadeh, 2003; Molnar & Tapponnier, 1977). While some authors have argued for a much earlier beginning of the collision (Allen & Armstrong, 2008; Ballato et al., 2011), most agree that the Arabia–Eurasia collision occurred during the early Miocene (on average 19 MYA; Ballato et al., 2011; Okay et al., 2010; Rogl, 1999) primarily in the area currently representing southern Anatolia, northern Syria, and Iraq (Darvishzadeh, 2003). During the middle Oligocene and early Miocene, prior to the plate collision, central Iran was covered by the Qom Sea, as indicated by biostratigraphic data and the extensive distribution of sediments of the Qom formation in central Iran basins (Daneshian & Dana, 2007; Ricou, 1994; Stocklin & Setudehnia, 1977). Deposits of the Qom Sea can today be found in the Dasht-e Kavir and Dasht-e Lut deserts in the central, eastern, and south-eastern regions of the country (Reuter et al., 2009). The Arabia–Eurasia collision created a wide zone of land deformation on the southern margin of Eurasia (Ballato et al., 2011; Okay et al., 2010) that is concurrent with the retreat of the Qom Sea from eastern Zagros in central Iran and the Tethys Sea from western Zagros.

The Arabia–Eurasia collision created the first land bridge between Africa and Eurasia (Darvishzadeh, 2003). This land bridge, well-known as the *Gomphotherium* land bridge, made the first faunal exchange between Eurasia and Africa possible (Harzhauser et al., 2007) and facilitated the range expansion and diversification of numerous taxa across Africa and Eurasia (Pook et al., 2009). There is evidence that early Proboscideans, endemic to Africa during the Paleogene, reached the Indo-Pakistani subcontinent during the earliest Miocene via the *Gomphotherium* land bridge (about 21–22 MYA; Antoine et al., 2003). The main wave of Proboscidean migration out of Africa started during the late Burdigalian (20.44 – 15.97 MYA) via the same path (Harzhauser et al., 2007). The effect of the *Gomphotherium* land bridge has been well-studied, e.g. in some examples of snakes. For instance, the split between the eastern and western species of the genus *Hemorrhois* likely occurred after the Arabia–Eurasia collision (about 19 MYA) and the formation of the *Gomphotherium* land bridge (Nagy et al., 2003; Wüster et al., 2008). According to fossil data of the elapid genus *Naja*, the Asian clade had split from the African clade at approximately 16 MYA (Rage & Szyndlar, 1990; Wüster et al., 2007). The early cladogenetic events within the snake genus *Echis* that gave rise to the four extant species groups took place at around 20 MYA, as did the inter-continental dispersal of the saw-scaled vipers (Pook et al., 2009). All these cases provide evidence for the profound biogeographical consequences of the formation of this land bridge.

III. Late Miocene: Uplift of Zagros and Alborz. The Arabia–Eurasia collision continued with a further uplift of the Zagros and the Alborz (Axen et al., 2001; Rezaeian et al., 2012; Ruban et al., 2007). Many authors place the main phase of folding and the uplift of the Zagros at about 11 MYA (e.g. Morley et al., 2009; Mouthereau, 2011; Mouthereau et al., 2012). Throughout the late Miocene and the beginning of the Pliocene (about 5 MYA), the Arabian Peninsula performed a progressive counter-clockwise rotation, which was associated with the formation of the Red Sea and the Gulf of Aden (Girdler, 1984), the uplift of the whole Iranian Plateau (15-12 MYA), and accelerated mountain formation at the northern and southern margins of the Iranian plate (Mouthereau et al., 2012). Central Iran rose from the Qom Sea, and a wide zone of land deformation appeared on the southern margin of Eurasia (Okay et al., 2010), which formed new habitats and drove the isolation and speciation processes of various taxa (Amer & Kumazawa, 2005; Macey et al., 1998; Pook et al., 2009; Stümpel, 2012). During the uplift of the Zagros, savannah-like habitats in north-western Iran disappeared and were replaced by mountainous landscapes (Ataabadi et al., 2011; Campbell et al., 1980).

IV. Quaternary and climate oscillations. The Pliocene was followed by a period of global climate oscillation and severe climatic changes worldwide, including Iran (especially in northern and western parts of the country; Kehl, 2009). Quaternary glacial and interglacial periods had direct effects on forming the distribution patterns of many species in the northern hemisphere (Hewitt, 1999, 2004). Facing dramatic climatic oscillations, the distribution range of species contracted into refugial areas or expanded. This 'Pleistocene species-pump' sped up extinction/speciation rates in many taxa. These effects of the Last Glacial Maximum (LGM; 21,000 - 19,000 years ago; Clark et al., 2009; Provan & Keith D. Bennett, 2008) are well understood in Europe and North America, but also to some extent in the case of Iran and Middle East.

The Middle East in general and Iran in particular (Ahmadzadeh et al., 2013; Javanbakht et al., 2017; Rajaei et al., 2013) likely represented an important refuge area for many species of otherwise more northern latitudes (now Europe) (Hewitt, 1999, 2004). Yet, the effects of the Pleistocene climate oscillations in the region itself remain far less well studied. During this period, the climate in northern and western Iran changed between dry and cold climatic conditions during the glaciation and moist and warm conditions during the interglacial periods (Clark et al., 2009; Ehlers & Gibbard, 2004; Kaufman et al., 2004). Palynological studies, for instance, show that changes in climate seasonality during the Quaternary period affected the dynamics of the Zagros Oak woodlands (Djamali et al., 2008; Stevens et al., 2001). Changes to the vegetation also affected the distribution patterns of faunal elements, especially insects (Adroit et al., 2018; Tóth et al., 2016). The most recent glaciation reached its maximum about 26,000 to 19,000 years ago, with strong impacts on the fauna and flora of Iran (e.g. Bihari et al., 2011; Nederi et al., 2014; Rajaei et al., 2013; Stümpel, 2012). Results of different studies confirm that the LGM led to much colder and more arid climate conditions in Iran compared to now (Djamali et al., 2011; El-Moslimany, 1986; van Zeist & Bottema, 1977; van Zeist & Wright Jr, 1963). The last glaciation also has changed the patterns of species distribution by dropping of the sea levels, for instance, caused the Persian Gulf to dry up and turned it into a land bridge between Iranian Plateau and the Arabian Peninsula facilitating faunal exchange between these two land masses (Büttiker, 1987). Rising of sea levels after the glaciation when the climate warmed have had a profound impact on the patterns of inter- and intraspecific variation among species (e.g. in the Brandt hedgehog, Yusefi et al., (2016)). The last glaciation ended with the Holocene Climatic Optimum between 9,000 to 5,000 years ago (Clark et al., 2009; Ehlers & Gibbard, 2004; Kaufman et al., 2004).

Biotic patterns

Biodiversity in numbers

The high abiotic heterogeneity and dynamic geology make Iran one of the most biodiverse regions in western Asia (Firouz, 2005; Noori et al., 2021; Rajaei et al., 2023; Yousefi et al., 2023). This relates not only to species richness but also to the high rates of endemism (Noroozi et al., 2019; Noori et al., 2023; Yousefi et al., 2023). Thus far, more than 1,327 species of vertebrates (including 559 birds, 309 species of freshwater fishes, 241 reptiles, and 196 mammals, 22 amphibians; (Esmaeili et al., 2018; Kaboli et al., 2016; Khaleghizadeh et al., 2017; Rajabzadeh, 2018; Safaei-Mahroo, 2019; Safaei-Mahroo et al., 2015; Yusefi et al., 2019 a & b; Darwish et al., 2023; Yousefi et al., 2023; Çiçek et al., 2024) and around 8,600 species of plants have been recorded, of which 13 % and 30 % are endemic, respectively (Ghahremaninejad & Nejad Falatoury, 2016; Noroozi et al., 2019). Despite existsnown high diversity, the real number of species, even in the better-studied taxa like mammals is believed to be underestimated and it is expected that many more species, yet unknown to science exist (Yusefi et al., 2019b).

This is even truer for invertebrates. The invertebrate fauna of the country is largely understudied, and the number of species and rates of endemism remain unclear (Rajaei et al., 2023). However, some groups are better catalogued (e.g., Arachnida with 1,146 species (Zamani et al., 2022) and Lepidoptera with 4812 species (Rajaei et al., 2023). Many more taxonomic revisions and smaller checklists have been published in recent years (e.g., Enayatnia et al., 2018; Khayrandish et al., 2017; Naderloo, 2017; Hodjat et al. 2018), but a general overview of the Iranian invertebrate fauna is not yet available.

Distribution of biodiversity – zoogeographic patterns

Iran has long been recognized by researchers as a zoogeographic transition zone (Yusefi et al., 2019a; Yousefi et al., 2023). The country is located on the intersection of three of the global zoogeographic realms (Holt et al., 2013; Ficetola et al., 2017): the two major mountain ranges, the Alborz and the Zagros, as well as the highlands of the northwest, are part of the Palearctic realm, whereas the Central Basin region belongs to Saharo-Arabian realm. The lowlands of the southeastern edge of the country represent the westernmost portion of the Oriental realm (Fig. 1a; Holt et al., 2013; Ficetola et al., 2017). This results in a complex mixture of taxa belonging to different biogeographic regions and it becomes visible in different taxa, with Palearctic species like red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), brown bear (*Ursus arctos*), and Eurasian lynx (*Lynx lynx*), , eruopean green woodpecker (*Picus viridis*), tawny owl (*Strix aluco*), Saharo-Arabian elements such as gazelles (*Gazella subgutturosa*, *G. bennettii*, *G. gazella*), cheetah (*Acinonyx jubatus*), sand fox (*Vulpes rueppellii*), and black-striped hairtail (*Anthene amarah*; Tshikolovets et al., 2014)and oriental representatives like Asiatic black bear (*U. thibetanus*), palm squirrel (*Funambulus pennanti*), Indian crested porcupine (*Hystrix indica*; Yusefi et al., 2019b), bay-backed shrike (*Lanius vittatus*), . sykes's nightjar (*Caprimulgus maharattensis*), striped Pierrot (*Tarucus nara*), Baphomet moth (*Creatonotos gangis*; Dubatolov & Zahiri, 2005; Tshikolovets et al., 2014).

Generally, Zagros Mountain from the northwest of the country toward the south and in parallel with the Ghohrud Mountain, in the margin of the central desert basins, limit the distribution of the Palearctic elements toward the extent of Saharo-Arabian and Oriental in the south of Iran. This pattern can be seen in some taxa such as Eurasian magpie (*Pica pica*), *Xanthorhoe wiltshirei* and *Pingasa lahayei*, which are distributed in the Palearctic realm, but they have their most southern distribution in Iran (Kaboli et al. 2011; Khaleghizadeh et al. 2017). Conversely, species like *Chazara briesis*, *Pieris ergane*, and *Turanana endymion* with Saharo-Arabian affiliation are limited to the northern seashores of the Persian Gulf in the country (Tshikolovets et al., 2014)

The specific geographical position and the unique topographical, climatic, and habitat diversity make Iran an interesting target for phytogeographic and zoogeographic studies. Hence, the use of faunal distribution data for assessing the biogeography of Iran has a long history (Yusefi, 2021). In fact, in the same year that Alfred R. Wallace wrote his opus on the geographical distribution of animals (Wallace, 1876), which established biogeography as a scientific subject (Lomolino et al., 2010), William T. Blanford, another prominent British naturalist, provided the first descriptive zoogeographical analysis of Iran based on his findings during a two-year expedition through the country (Blanford, 1876). Further studies followed, but unlike phytogeography (White & Léonard, 1991; Fig. 4a), which largely followed the three main macro-bioclimatic zones (Temperate, Mediterranean, and Tropical) identified by Djamali et al. (2011), zoogeographers failed to find any consistent pattern. Blanford (1876) subdivided Iran into five zoogeographical regions based on vertebrate faunal distributional ranges: 1) Central Plateau, 2) Caspian/Hyrcanian Forest, 3) Zagros Woodlands, 4) Mesopotamian Area, and 5) Persian Gulf and Baluchistan Shores (Fig. 4b). Years later, Zarudny (1911) classified the bird fauna of Iran into nine zoological zones, whereas (Scott et al., 1975) recognized only eight main regions for birds. The Iranian ichthyofauna has been categorized into nineteen main basins (Coad, 1985), and thirteen zoogeographical regions have been identified for the reptiles by Anderson (1968).

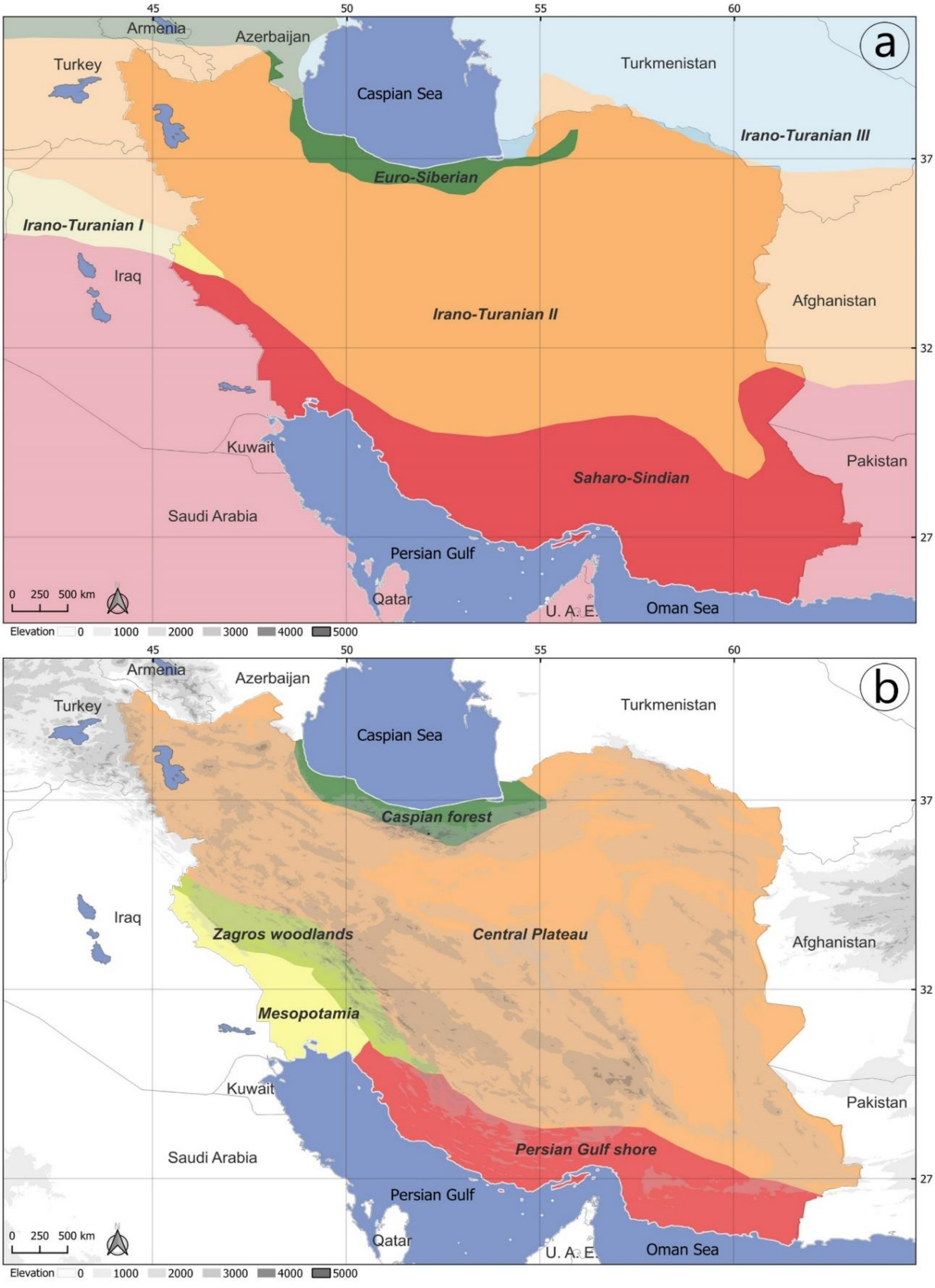

Figure 4. a) Phytogeographic (adopted from White and Léonard 1991) and b) zoogeographic subdivisions of the country based on mammal's data (adopted from Blanford 1876).

In invertebrates, only a few preliminary biogeographical studies are available. Naumann (1987) studied the geographic distribution patterns of the genus *Zygaena* in the Middle and Near East. This study proposed three eco-geographical types of habitats of this genus: 1) Arboreal elements (in the Alborz and Zagros), 2) Eremic elements (in the steppe areas with *Astragalus*/*Artemisia* vegetation), and 3) Oreal elements (at the high elevations of the Alborz and the north-west Zagros). Dubatolov and Zahiri (2005) and Matov et al. (2008) conducted more detailed biogeographical analyses to assess distribution patterns of tiger moths (Arctiinae) and heliothine moths (Noctuidae). Dubatolov and Zahiri (2005) suggested three main territories: western, northern and central regions that are mainly occupied by Palearctic fauna, the northern seashores of the Persian Gulf inhabited by Paleotropical elements (e.g. *Utetheisa lotrix*, *Argina astrea*) and the most southeastern parts by Oriental species (e.g. *Creatonotos gangis*). Paknia and Pfeiffer (2011) applied hierarchical cluster analysis on distribution data of ant species and suggested four distinct ecoregions: 1) Alborz (Range Forest steppe), 2) Central (Persian desert basins), 3) Zagros (Mountain Forest steppe), and 4) Nubo-Sindian (from the Khuzestan plain to Makran and Baluchestan region). This zoogeographical pattern somehow indirectly represents the identified global ecoregions recognized by Dinerstein et al. (2017), representing the most distinctive examples of biodiversity for a given major habitat type that is identified within each biogeographic realm. In another study, based on the distribution patterns of Fulgoromorpha (family Auchenorrhyncha), Mozaffarian (2013) identified three main biogeographic regions and 13 primary zones and suggested six endemic zones of this group: 1) Caspian zone, 2) southern slopes of Alborz, 3) Zagros, 4) Kerman Mountains, 5) Khorasan Mountains, and 6) Baluchistan and Persian Gulf coast.

Most of the studies mentioned above were based on only a few taxa without using descriptive /qualitative approaches and yielded very incongruent results. Yusefi et al. (2019b), however, applied two different analytical approaches, including conventional hierarchical clustering based on species turnover (Kreft & Jetz, 2010) and a novel network-based infomap algorithm (Edler et al., 2017) on distribution data of 186 terrestrial mammals. Their results showed good agreement in bioregionalization between the methods, but the distance-based method detected five bioregions, while the network method detected seven bioregions: 1) Alborz-Zagros-Kopet Dag, 2) Central Basin, 3)Baluchestan-Khorasan, 4) Persian Gulf Shores-Khuzestan, 5) Makran Mountains, 6) Turkmen Plain, 7) Makran lowlands and two transition zones (Abarkooh-Shahreza ridges and Arvand-Shadegan lowlands). A major difference between the results of these two approaches was that the network method detected more bioregions, especially within the Central Basin, while the distance-based method highlighted two distinct regions in the north: N Zagros-Caucasus and Hyrcanian. According to

Yusefi et al. (2019a), the mammal distribution follows a complex pattern which is reflected in the high number of biogeographical units at small spatial scales, each of which is composed of a unique combination of species.

Distribution of biodiversity – phylogeographic patterns

Looking at genetic data, patterns even become finer scaled. So far, only a little genetic data is available, and the few available studies are fragmentary and mostly based on a single or few species and genetic markers (e.g., Ahmadzadeh et al., 2013, 2017; Paknia & Rajaei, 2015). Thus, compared to other regions such as Europe and North America, phylogeographical studies in Iran (like most Middle Eastern countries) are far from showing a comprehensive pattern. Nevertheless, the few studies available on some vertebrate species have emphasized two main points: first, the important role of mountain range uplift in shaping the current genetic makeup of species by acting as a barrier and/or corridor (e.g., Ghaedi et al., 2021; Yousefi et al., 2023), and second, the important role of the country as glacial refugia during the Pleistocene (e.g., Djamali et al., 2012; Paknia & Rajaei, 2015).

Several studies show that the uplifting of the Zagros and Alborz Mountain ranges acted as a barrier to gene flow for some taxa and, at the same time, as a corridor for the migration of others (e.g. Ghaedi et al., 2021; Sanmartín, 2003). This mostly happened in the context of the collision of the Arabian tectonic plate with Eurasia (35-20 MYA), during the mid-Miocene (10-12 MYA) and late Miocene (around 6-7 MYA; Mouthereau, 2011). The barrier effect between Afro-Arabia / Mesopotamia and the Iranian Central Basin was shown, e.g. in lacertids (Lacertidae, Reptilia), where the isolation of *Mesalina watsonana* from its congeners and the separation of *Eremias montanus* from *E. persica* were attributed to the Zagros uplifting (Ahmadzadeh et al., 2017). They showed that these two species went through a similar diversification event in response to geographical processes in the plateau associated with mountain uplifting. According to this study, the first divergence of *E. persica* coincides with the uplift of the Zagros in the west of the country in the mid-Miocene (about 13 MYA), while the original divergence in *M. watsonana* goes back to the uplifting of the Alborz in the north (about 6.6 MYA) at the border between the upper Miocene and the Pliocene. Ghaedi et al. (2021) found the same pattern in the diversification of two species in the genus *Saara* from central Iranian Plateau (*S. asmussi*) and Mesopotamia (*S. loricata*), which were separated by starting orogeny events in the Zagros during the Pliocene.

On the other hand, the Alborz acts as a corridor for sharing faunistic elements among the northwest, south of the Caspian Sea, and the northeastern regions; examples come from the Persian fat dormouse

(*Glis persicus)* and the Caucasian pit viper (*Gloydius halys caucasicus*), which are distributed throughout the Alborz Mountains from the Transcaucasia region towards Turkmenistan and the northwest of Afghanistan, respectively (Asadi et al., 2019; Kryštufek et al., 2021).

Several regions of the country have served as refugia for a range of taxa. For example, the southern Caucasian region in the northwest has been suggested as the ancestral range of some Palearctic species and acted as a Pleistocene refugia, which led to the long-term isolation of different species from northern latitude and western longitude. This is for example the case for the Satyrine butterfly *Proterebia afra* (Bartonova et al., 2018), the black alder *Alnus glutinosa* (King & Ferris, 1998), the meadow grasshopper *Chorthippus parallelus* (Cooper et al., 1995), the honeybee *Apis mellifera* (Han et al., 2012), the domestic mouse *Mus musculus* (Boursot et al., 1993), and the Cynipid gall wasp *Synergus umbraculus* (Bihari et al., 2011). In addition, an examination of the global phylogeography of the spongy moth (*Lymantria dispar* L.) using several genetic markers revealed the presence of a distinct mitogenomic lineage endemic to the Transcaucasia region (Zahiri et al., 2019). This study demonstrated that the populations from Transcaucasia contain the highest mitochondrial haplotype diversity among spongy moth populations, potentially indicative of an ancestral area for the entire *dispar*-group. The analysis of mtDNA showed very low divergence within *L. dispar* across most of the native range except for specimens from Alborz and Zagros, eastern Iraq, and parts of the Caucasus (Talysh Mountains and north Caucasus), which formed a highly divergent assemblage. The timing and location of dispersal events indicated an initial eastward expansion through modern-day Russia, into central Asia, and continuing to the Pacific coast around 1.3 MYA. Divergence times also indicated expansion into Europe via northern Caucasia around 1.1 MYA, concomitant with other major changes in Europe's flora and fauna (Blain & Bailon, 2019). Similarly, genetic analysis of a cosmopolitan weevil pest (*Hypera postica*) also revealed a high diversity and potential origin in northwest Iran (Sanaei et al., 2016, 2021).

The Hyrcanian forest on the southern coast of the Caspian Sea also has been defined as a refuge area for several species during the Pleistocene glaciation. Evidence for glacial refugia of the Hyrcanian forest comes predominantly from palynological data (Djamali et al., 2008; Leroy et al., 2013) and phytogeographic studies (Akhani et al., 2010). However, this area has also been reported as refugia for several faunal elements, including the Persian medical leech *Hirudo orientalis* (Darabi-Darestani et al., 2018), the tree frog *Hyla orientalis* (Gvoždík et al., 2010), the freshwater crab *Potamon ibericum* (Parvizi et al., 2018), the Caucasian pit viper *Gloydius halys caucasicus* (Asadi et al., 2019) and the fat dormouse *Glis glis* (currently *persicus*) (Nederi et al., 2014). This is partly because of the eustatic changes of the Caspian Sea (a remnant of the Tethys Sea) during the late Cenozoic that had a great influence on the paleogeography of the region (Atamuradov, 1994). Besides being a refugium, this region shares several faunal elements with two neighboring areas in the north-west (Transcaucasia and the South Caucasus) and north-east (the Turkmen Plain and Kopet-Dag Mountains). Furthermore, the northeastern regions harbor some unique faunistic elements and share some taxa with Central Asia (Schneider et al., 2018). Some taxa showed higher diversification and haplotype turnover in these two regions (Asadi et al., 2019; Nederi et al., 2014; Parvizi et al., 2018).

Besides the important role of Alborz and Zagros uplifts in shaping the current genetic makeup of species by acting as a barrier, other mountains such as Kopet-Dag in the northeast and Makran in the southeast limited the distribution ranges for many taxa in the Iranian Plateau. It has been also suggested that some isolated mountains in the Central Basin, particularly in Kerman and Yazd with elevations higher than 4,000 m, acted as distinct islands of biodiversity surrounded by desert (Mozaffarian, 2013; Noroozi et al., 2018). These mountains with a high rate of endemism (e.g. Keil, 2014; Noroozi et al., 2019) already have been mentioned as distinct zoogeographical regions by some authors (e.g. Yusefi et al., 2019a; Zarudny, 1911), and have been suggested as potential refugia for some species during the glacial periods (e.g. planthoppers (Fulgoromorpha), Mozaffarian, 2013).

Future directions

Lack of Knowledge

Despite being far from complete, the currently available knowledge of vertebrate fauna and its distribution patterns is useful to draw biogeographical inferences. However, our knowledge of the invertebrate fauna is still fragmentary and insufficient (Rajaei et al. 2023). There are some recent advances in updating the catalogues of Iranian invertebrates (e.g., Naderloo, 2017; Zamani et al. 2022; Rajaei et al. 2023). However, there are not even reliable updated checklists for most groups of arthropods and the distribution patterns of most species remain unknown. This gap causes a superficial understanding of the zoogeographical subzones for this diverse group and thus, most of what we know is only descriptive and based on non-statistical evaluations. This is specifically important considering the high conservation demands of many regions as anthropogenic pressure constantly rises threatening unique biodiversity communities. Hence, there is an urgent need to perform more systematic faunal surveys, especially for invertebrates to understand their diversity and distributions to be able to more effectively not only protect vertebrate diversity, but also the regions with high insect diversity. For this, more taxonomic and faunistic studies are required, which further should be supplemented with DNA barcoding data to provide a comprehensive basis for future conservation management.

Lack of comprehensive taxonomic inventories and taxonomists

Although species have long been considered the basic units of biodiversity (Claridge, 2010), the issue of how best to delimit species, as the central bottleneck for any further study, remains controversial. It is even more complicated when it comes to a mega-diverse group like Arthropoda, the most diverse group of organisms in the whole history of life (Grimaldi et al., 2005), and a country of incredibly high arthropod biodiversity, such as Iran, where our taxonomic knowledge has a long way to be completed. For several centuries, morphological characters were applied solely for species identification. However, these methods are problematic and extremely time-consuming, often due to the lack of an appropriate methodology to quantify shape variation (Arnqvist, 1998) and to questionable homology assessments. On the other hand, the number of experienced taxonomists is decreasing (Bacher, 2012; Hopkins & Freckleton, 2002) for many groups of organisms. This is a major dilemma not only for taxonomy but also for any related fields (e.g. ecology, biogeography, conservation biology, etc.), especially in the epoch of the Anthropocene, when biodiversity is dramatically declining.

Lack of comprehensive DNA barcode reference libraries

While there is a lack of taxonomic and faunistic data on invertebrates in Iran this is even more severe when it comes to molecular data. Unfortunately, a large proportion of the fauna of the country, in particular arthropods, remains undescribed and we still do not know how many species exist. DNA identification techniques can be a solution to overcome the taxonomic impediment that often results from either the lack of biodiversity strategic plans or political reasons. DNA barcoding — mitochondrial cytochrome *c* oxidase subunit 1 gene (COI) — has gained diverse applications in biodiversity science since its inception in 2003 (Hebert et al., 2003). This gene region is generally characterized by low intraspecific variation and much higher divergence between species. As a consequence, by assembling sequence data for known species (i.e., a DNA barcode reference library), newly encountered specimens can be assigned to a species by comparing their COI barcodes to those in the library. These DNA database archives are curated and publicly available on BOLD, the Barcode of Life Data Systems (Ratnasingham & Hebert, 2007). Although these libraries are approaching completeness for some groups of vertebrates and invertebrates in certain geographic realms, like North America and Europe, no major taxonomic group has seen a similar analysis in Iran.

There are currently 12,748 specimen records from Iran available in public DNA databases (e.g., BOLD and GenBank), of which 11,969 record entries contain DNA sequence data of various gene regions, 11,796 of which are COI (contains both COI-5P and COI-3P fragments; as of January 2023). In total, arthropods cover 54% of the barcode data followed by vertebrates (27%; Fig. 5). This dataset contains 11 Phyla, 32 Classes, 144 Orders and 10,057 genera. Globally more than 619,794 BINs (Barcode Index Number; Ratnasingham & Hebert, 2013), i.e., barcoding-delimited operational taxonomical units (OTUs) for the animal kingdom exist in public databases (as of January 2023). The total number of existing BINs for the fauna of Iran is 2,297 BINs representing 3,167 described species and 14,498 specimen records that are deposited in 149 institutions. Considering that more than 1,000 species of spiders and almost 5,000 species of butterflies have been recorded for Iran already, the lack of comprehensive data is more than evident. More taxon-specific local studies, or even better a nationally coordinated activity such as in Canada or many European countries are needed to close this gap in the future.

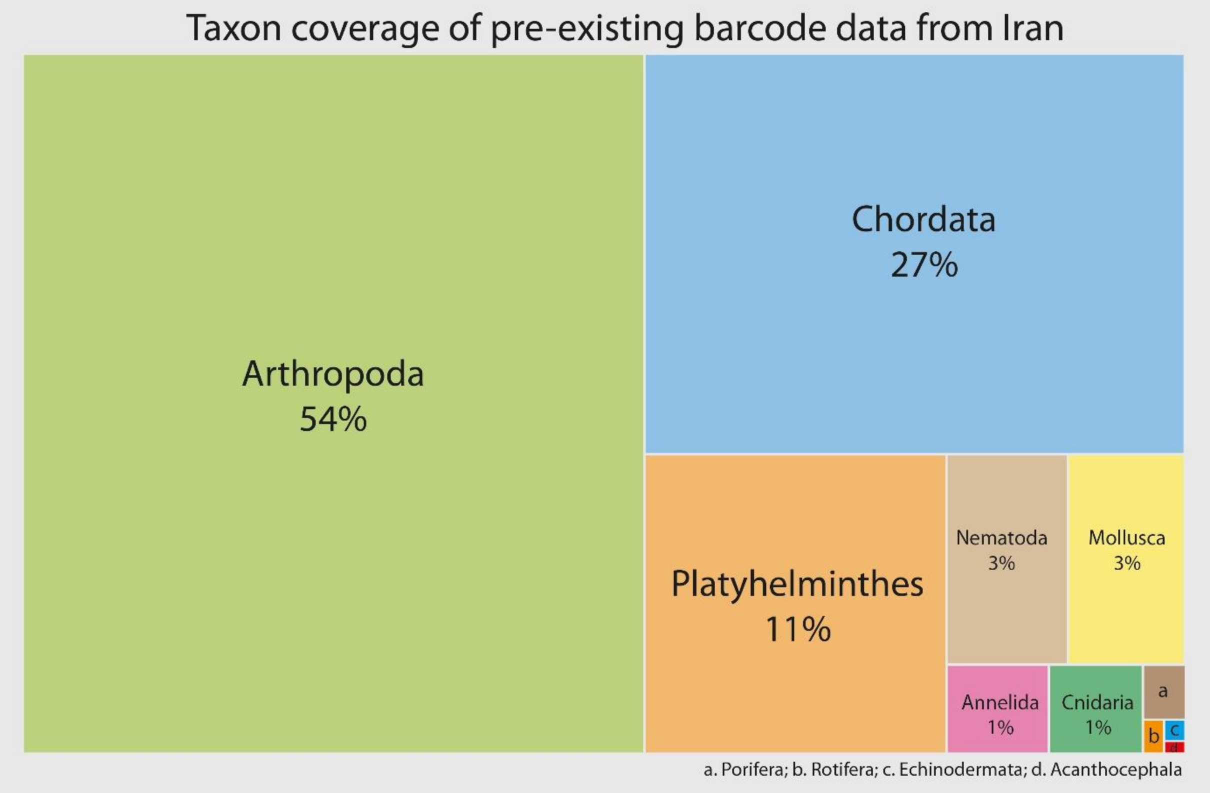

Figure 5. Taxon coverage for 11,796 pre-existing COI (including DNA barcode region) records of Iranian fauna in public DNA repository databases (BOLD and GenBank).

The BIN system represents a partial solution as it circumvents the taxonomic impediment. Specimens can be assigned to OTUs or BINs, an effective proxy for species, enabling large-scale, comprehensive assessments of diverse animal assemblages (Hebert et al., 2016). After assembling DNA reference libraries for the major lineages of the Iranian fauna, these may provide a good basis for comparison with comprehensive reference libraries from the Palearctic and other zoogeographical regions for biodiversity analyses. This may allow us not only to better understand the patterns of zoological diversity in one of the most complex biogeographical transition zones but also to reveal biogeographic divisions in less well-known parts of the world.

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- Chapter II

Georeferencing historical occurrences

A gazetteer of elusive localities of Iranian Lepidoptera records

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During the last two centuries, the Lepidoptera of Iran have mainly been investigated by European and Russian entomologists, with authors such as Ménétries, Lederer, Christoph, Pfeiffer, Brandt, Amsel, Ebert and others publishing large amounts of data from different localities around the country. Depending on the original language of the author, some of the visited localities were recorded with different spellings (e.g., Booshehr, Bouchir, Buschehr and Bushire for Bushehr), and finding such names on maps can be quite an elaborate process.

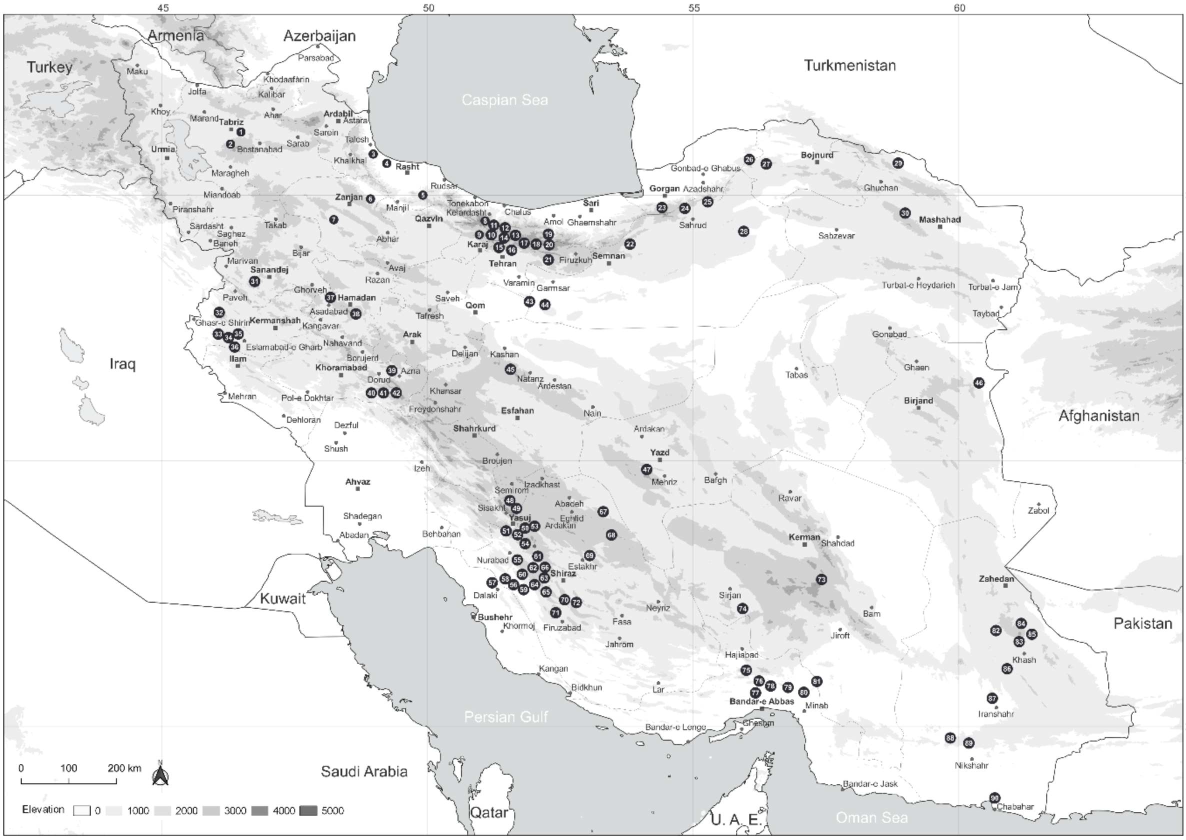

Figure 1. Map of Iran including names of province capitals and some important cities. Numbers refer to the most elusive Iranian localities found during the compilation of this catalogue.

Additionally, a number of cities and villages in the old literature have been renamed over time (e.g., Gorgan as the new name of Astarabad or Jiroft as the new name of Sabzewaran). Moreover, and in the absence of precise geographic coordinates, early entomologists simply obtained local names from the local people, writing down what they heard based on the local pronunciations. Some of these spellings are quite different from what is found on maps today (e.g., Comée for Komehr, Fars prov.). Sometimes, colloquial names absent on maps were given (e.g., Sineh Sefid in Fars prov., a mountain foot close to Dasht-e Arjan in W Shiraz). Pinpointing such localities on maps is sometimes extremely challenging, even for native Iranian researchers or tour guides.

During this project, we amassed a long list of such place names and georeferenced them. These localities are listed alphabetically in Appendix 1 together with all unique variants found in the literature. All localities were assigned geographic coordinates and assigned to their relative provinces. Extremely elusive localities or historically important sampling sites were assigned numbers (in parentheses), which were plotted on the map in Fig. 1 & Table 1. These numbers are plotted from northwest to southeast. An asterisk (*) marks cities or villages frequently referred to in the literature. An interactive version of the map is available at: https://shorturl.at/bdiY6.

Table 1. The list of the extremely elusive localities or historically important sampling sites for Lepidoptera of Iran.

Number	Location	Alternative or old names	Province	Latitude/°N	Longitud /°E
1	Pineh Shalvar		Azerbaijan-e Sharghi	37.989	46.367
2	Sahand Mt.		Azerbaijan-e Sharghi	37.723	46.351
3	Asalem		Gilan	37.717	48.960
4	Bandar Anzali	Anzali, Bandar-i Anzali, Bandar-e Anzeli, Bandar-e Pahlavi, Bandar Pahlavi, Bandar Pahlawi, Enzeli	Gilan	37.464	49.481
5	Amarlu	Jirandeh	Gilan	36.762	49.804
6	Sendan Mt.	Kuh-e-Sendan	Zanjan	36.700	48.751
7	Arkaun		Zanjan	36.303	48.129
8	Sardab Tal		Mazandaran	36.399	51.132
9	Arangeh		Alborz	35.939	51.072
10	Asara	Assara	Alborz	36.038	51.196
11	Kandovan Tunnel	Kandavan, Kandovan, Kendevan	Alborz	36.141	51.307
12	Nesa	Nissa	Alborz	36.078	51.318
13	Dizin	Dezen	Alborz	36.045	51.418
14	Tochal	Tocal, Totschal	Tehran	35.884	51.419
15	Evin		Tehran	35.797	51.379
16	Darband		Tehran	35.823	51.425
17	Shemshak	Chemchak, Shimshak	Tehran	35.931	51.527
18	Polour	Polur	Mazandaran	35.849	52.050
19	Rineh		Mazandaran	35.880	52.169
20	Ab-e Ask	Ab Ask	Mazandaran	35.868	52.145
21	Tar Vally		Tehran	35.730	52.132
22	Ahuan Pass		Semnan	35.754	53.720
23	Jahannama		Golestan	36.612	54.330
24	Shahkuh	Shahkuh	Semnan	36.513	54.703

25	Khoshyeylagh		Golestan	36.848	55.357
26	Golestan National Park	Shahabbad National Park, Shahabbad National Park, Mohamad Reza Shah National Park	Golestan	37.395	55.801
27	Dasht-e Mirzabailoo	Mirza Boyloo, Dasht-e Mirza Boyloo	Khorasan-e Shomali	37.350	56.233
28	Biarjomand	Biyarjomand	Semnan	36.081	55.811
29	Kopet Dag Mt.		Khorasan-e Razavi	37.368	58.719
30	Binaloud Mt.	Binaloud, Kouh-i-Binaloud, Kuh-e Mirabi, Mirabi Mt., Binalud, Mount	Khorasan-e Razavi	36.426	58.849
31	Ariz		Kordestan	35.375	46.856
32	Pa Tagh		Kermanshah	34.432	46.018
33	Sar Mil		Kermanshah	34.342	46.128
34	Harir		Kermanshah	34.310	46.200
35	Kerend-e Gharb	Kerend, Karind	Kermanshah	34.281	46.236
36	Ghalaje Pass		Kermanshah	33.962	46.326
37	Asadabad Pass		Hamadan	34.828	48.183
38	Alvand Mt.		Hamadan	34.664	48.487
39	Kohyeh		Lorestan	33.368	49.223
40	Naryman	Narmiyan	Lorestan	33.171	49.000
41	Gahar Lake		Lorestan	33.302	49.285
42	Partsehe Kabud		Lorestan	33.248	49.414
43	Dasht-e-Kavir		Qom	34.943	51.775
44	Salt Lake	Salzsee, Salt-Lake	Qom	34.702	52.066
45	Ghohrud		Esfahan	33.667	51.418
46	Kuh Mirza Arab Mt.		Khorasan-e Jonubi	33.229	60.240
47	Barfkhaneh	Barf Khaneh Mt.	Yazd	31.548	54.147
48	Dena Mt.	Kuh-i-Dinar, Dinar Mt.	Kohgiluyeh va Boyer-Ahmad	30.950	51.433
49	Gardaneh Bijan	Bijan Pass		30.875	51.508
50	Yasuj	Yassudj, Yassuj, Yesuj, Yasooj	Kohgiluyeh va Boyer-Ahmad	30.668	51.588
51	Tal-e Khosrow	Tal-i-Khosroe, Tal-i-Khosrow, Tall Khosrow, Talochosroe, Tal Khosro	Kohgiluyeh va Boyer-	30.606	51.584

			Ahmad		
52	Tang-e-Sorkh	Tang-e-Sorkh, Tange Surkh, Tange Surkh	Kohgiluyeh va Boyer-Ahmad	30.436	51.764
53	Komehr	Comee, Comehr	Fars	30.446	51.878
54	Barm-e Firuz	Barme Firouz, Barm-i-Firus, Barm-i-Firuz, Barm-i-Firuz Mt.	Fars	30.399	51.944
55	Shapur	Bischapur, Bishapur	Fars	29.778	51.571
56	Kamaraj	Kamarij, Kamarej, Kemaredj	Fars	29.610	51.477
57	Dalaki bridge		Bushehr	29.467	51.314
58	Cherrun	Charoum, Choroum, Tchoureum, Tschouroum	Fars	29.587	51.432
59	Imam Sade	Imam Zadeh	Fars	29.530	51.820
60	Dasht-e Barm	Dasht-i-Barm, Pusht-i-Bam	Fars	29.556	51.889
61	Dasht-e Arjan	Dachte-Arjan, Daschte Ardjan, Dascht-e Arzan, Dasht-Ardjan, Dasht-e Arzhan, Dasht-Arjan	Fars	29.654	51.981
62	Miyan-Kotal	Fort Mian Kotal, Fort Miyan Kotal, Mian Kotal	Fars	29.563	51.914
63	Sine Sefid	Fort Sine-Sefid, Sineh Sefid	Fars	29.570	51.920
64	Kotal-e Pirezan	Kotal Pirezan, Pir-e-Zan, Pir-i-Zan, Kotal-Pirehzan	Fars	29.554	51.926
65	Dishak Mt.		Fars	29.537	51.975
66	Khan-i-Zinian		Fars	29.674	52.148
67	Gardaneh ye Kuli Kosh	Kuli Kush Pass, Quli Kush Pass, Qulikush, Quli-Kush, Kowli Kosh	Fars	30.802	53.164
68	Didegan		Fars	30.365	53.321
69	Takht-i-Jamshid	Persepolis	Fars	29.934	52.891
70	Hanifaqan	Hunaifagan	Fars	29.092	52.560
71	Tang-e Ab		Fars	28.956	52.552
72	Muk-Pass	Mook-Pass, Shahrak-e Muk	Fars	29.094	52.658
73	Taj Khoros Mt.		Kerman	29.526	57.275
74	Godar		Kerman	28.978	55.791
75	Sar Chahan		Hormozgan	28.001	55.859
76	Sardze	Sarzeh	Hormozgan	27.565	56.119
77	Genu Mt.	Hormozgan	27.37	27.370	
78	Issin	Isin	Hormozgan	27.317	56.314
79	Schirin Rud		Hormozgan	27.415	56.695
80	Gourband		Hormozgan	27.325	56.980

81	Rudan	Roodan, Dehbarez	Hormozgan	27.606	57.188
82	Eskelabad		Sistan-o-Baluchestan	28.564	60.800
83	Kusheh	Kute	Sistan-o-Baluchestan	28.538	60.998
84	Taftan Mt.	Kuh-e-Taftan, Kouh-i-Taftan, Koh-i-Taftan, Kuh-i-Taftan	Sistan-o-Baluchestan	28.600	61.133
85	Sangan	Fort Sengan, Sengan	Sistan-o-Baluchestan	28.566	61.267
86	Karvandar		Sistan-o-Baluchestan	27.845	60.769
87	Rig-e Kaput	Rig-Kabud	Sistan-o-Baluchestan	27.209	60.472
88	Tange-Sarheh	Tang-e Sarhad	Sistan-o-Baluchestan	26.545	59.940
89	Takht-e Malek	Tahte Malek, Takht Malek	Sistan-o-Baluchestan	26.448	60.048
90	Tis		Sistan-o-Baluchestan	25.354	60.626

- # Chapter III

Insight into the general patterns of Lepidoptera

General patterns of the Lepidoptera fauna of Iran

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The main purpose of this catalogue was to improve our knowledge of the Lepidoptera fauna of Iran and acquire a better knowledge of the patterns of distribution of this large insect order within the country. These patterns not only show the large-scale structure of the faunal elements of this order in Iran, but also highlight research gaps and other needs in Iranian lepidopterology, which should be addressed before we lose more habitats and species.

This chapter addresses questions such as: How many lepidopteran species are reported from Iran? How many of them are truly present in Iran? I.e., how many need further confirmation and how many have been erroneously reported? How many of the reported species are regarded as synonyms today? How are they systematically distributed (e.g., how many species are known per family)? How are they geographically distributed, both horizontally and vertically? Which taxonomic groups are especially in need of additional sampling efforts and taxonomic revisions? Finally, how many are endemic to Iran?

Species diversity

In total, 6,191 species-level names are listed in this catalogue as reported from Iran in the literature or for the first time in the present catalogue. Of these, 1,262 are regarded as junior synonyms and 117 as erroneously reported, although 24 are considered likely to occur in the country (see Appendix 1). Of the 4,812 remaining valid species, 4,517 are regarded as definitely resident in Iran, whereas 295 need further confirmation [see Fig. 1 and notes in Rajaei et al. (2023)].

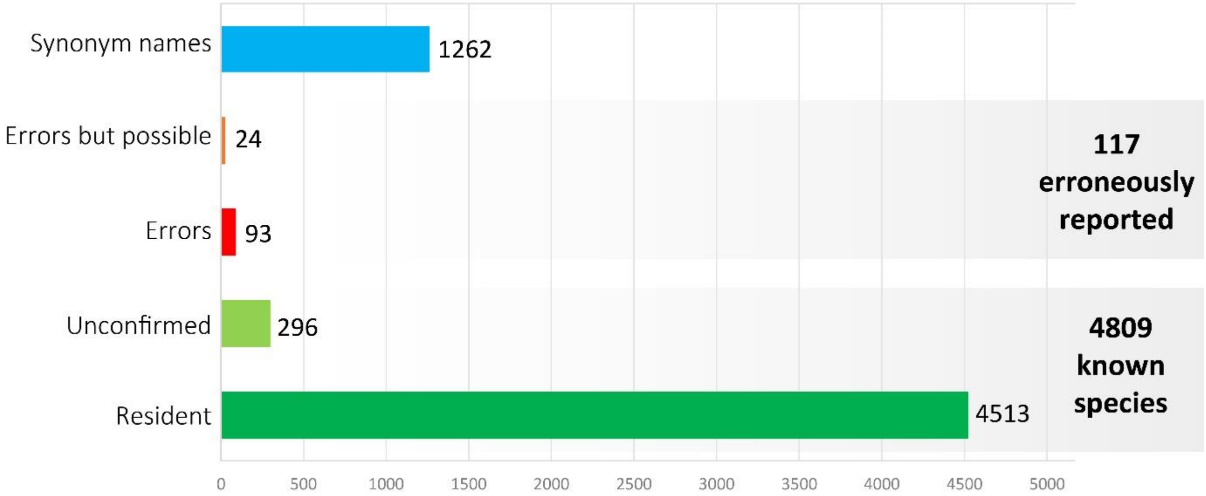


Figure 1. Summary of the statuses in Iran of the lepidopteran species listed in this catalogue.

In total, we list 892 endemic species for Iran, corresponding to an endemicity rate of 19.7% (Appendix 2). As can be observed in Fig. 2, over 70% of the endemic species have been collected at altitudes between 1,000 and 3,000 m. Isolation, by reducing gene flow, is an important driver of speciation, and higher per-species speciation rates caused by increasing isolation with elevation are assumed to be one of the most plausible explanations for the globally consistent pattern of higher endemism at higher elevations (Steinbauer et al. 2016). Phylogenetic evidence indicates that many high-elevation endemics across the globe are phylogenetically young taxa resulting from recent rapid diversification, e.g., in the New Zealand Alps (Winkworth et al. 2005), the Andes (Hutter et al. 2013) and East Malaysia (Merckx et al. 2015). These localized areas (i.e., type localities) can be used as a reference for future conservation initiatives.

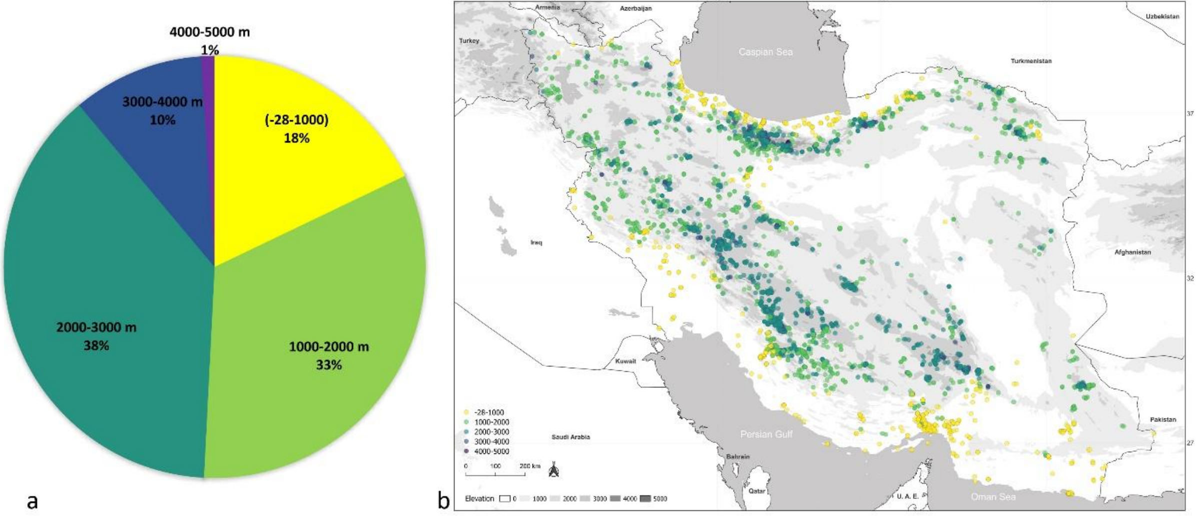
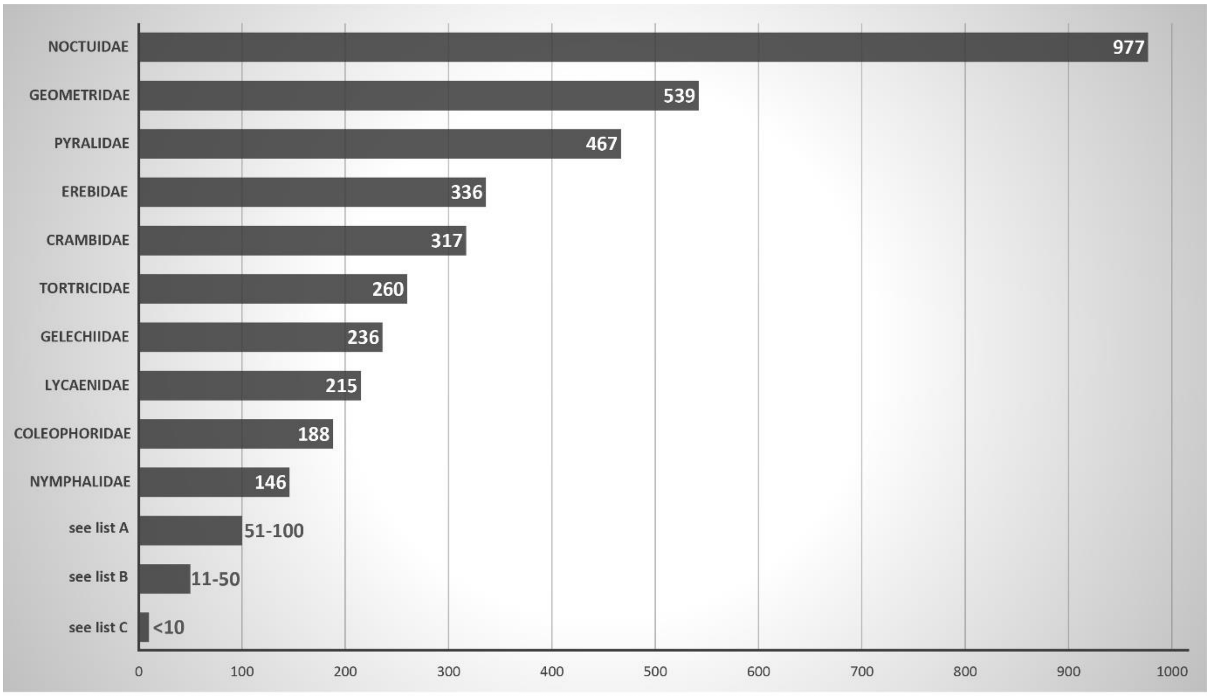


Figure 2. Elevational diversity gradients of the endemic Lepidoptera species of Iran. In (b), each dot represents a species



List A: AUTOSTICHIDAE, COSSIDAE, DEPRESSARIIDAE, GRACILLARIIDAE, PIERIDAE, PTEROPHORIDAE, SESIIDAE, TINEIDAE, ZYGAENIDAE.

List B: ALUCITIDAE, AUTOSTICHIDAE, BRACHODIDAE, BUCCULATRICIDAE, COSMOPTERIGIDAE, COSSIDAE, DEPRESSARIIDAE, ELACHISTIDAE, GRACILLARIIDAE, HESPERIIDAE, LASIOCAMPIDAE, MEESSIIDAE, NEPTICULIDAE, NOLIDAE, NOTODONTIDAE, OECOPHORIDAE, PAPILIONIDAE, PIERIDAE, PSYCHIDAE, PTEROPHORIDAE, SCYTHRIDIDAE, SESIIDAE, SPHINGIDAE, TINEIDAE, YPSOLOPHIDAE, ZYGAENIDAE.

List C: ADELIDAE, ARGYRESTHIIDAE, BATRACHEDRIDAE, BEDELLIIDAE, BLASTOBASIDAE, BOMBYCIDAE, BRAHMAEIDAE, CARPOSINIDAE, CHOREUTIDAE, CIMELIIDAE, DOUGLASIIDAE, DREPANIDAE, EPERMENIIDAE, EPIPYROPIDAE, ERIOCOTTIDAE, EUTELIIDAE, GALACTICIDAE, GLYPHIPTERIGIDAE, HELIODINIDAE, HELIOZELIDAE, HEPIALIDAE, LECITHOCERIDAE, LIMACODIDAE, LYONETIIDAE, LYPUSIDAE, MICROPTERIGIDAE, MOMPHIDAE, PLUTELLIDAE, PTEROLONCHIDAE, SATURNIIDAE, STATHMOPODIDAE, TISCHERIIDAE, USTYURTIIDAE, YPONOMEUTIDAE.

Figure 3. Number of known Lepidoptera species per family in Iran.

Distribution of species within families

As can be observed in Appendix 1, some families are more species-rich than others. However, this pattern could simply be an artefact due to some taxonomic groups being less studied (e.g., the microlepidopteran families) when compared to other parts of the world (e.g., Europe or North America). In contrast, some families (e.g., Zygaenidae, Cossidae and nearly all Papilionoidea) are much better known. Fig. 3 shows the number of species per family in Iran.

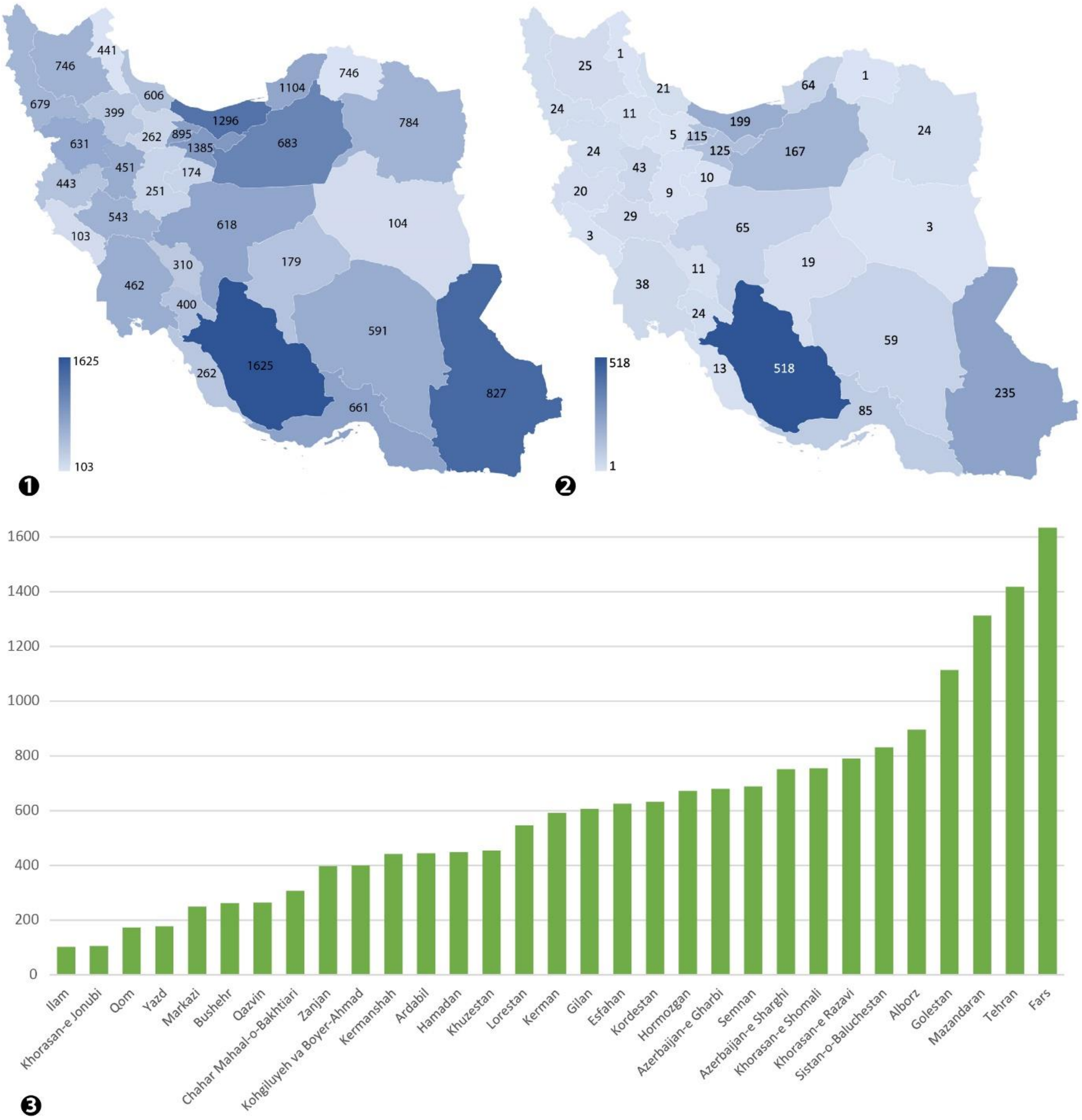


Figure 4. Data on Iranian Lepidoptera, subdivided by province. **a**. Map showing number of recorded species per province. **b**. Map showing number of type localities per province. **c**. Bar chart showing number of recorded species per province.

Horizontal and vertical distribution of Lepidoptera species in Iran

Not only have some lepidopteran lineages been incompletely studied in Iran (e.g., most microlepidopteran families), but some provinces have been insufficiently explored overall. The number of recorded species per province is shown in Appendix 3 and Fig. 4, where it is clear that several provinces (e.g., Ilam and Khorasan-e Jonubi) have been largely neglected in past taxonomic surveys. Of note, the Ilam province is located in a transitional zone between the Zagros Mountain and the desert plains of Iraq, and potentially contains a rich Lepidoptera fauna. Some other provinces (e.g., Ardabil and Khorasan-e Shomali), although much better studied, show a low number of type localities (Fig. 4b), which could be explained by intensive taxonomic studies on the other side of the national borders of Iran, e.g., in the Kopet-Dagh Mountain (Turkmenistan) and Azerbaijan Mountain (Azerbaijan).

Most lepidopterous larvae feed on living plants, many of them on a single plant species (monophagous) or a few related species (oligophagous), and their distribution is therefore dependent on the distribution of their host plants. Areas with a high diversity of plants have, in most cases, a correlatively high diversity of Lepidoptera. In some families of Lepidoptera (e.g., Gracillariidae, Tortricidae and Geometridae), the larvae of a majority of species feed on the leaves of deciduous trees. These families are thus most diverse in forested areas such as mountains and north-facing hills. The larvae of many species of Gelechiidae, Pyralidae and Noctuidae feed on low plants, often in dry areas, and these families are most diverse in steppes and semi-deserts.

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- Chapter VI

Bioregions of Iranian Lepidoptera

Biogeographic patterns in a transition zone: a case study on Iranian Lepidoptera

Submitted in Diversity and Distribution

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Abstract

Aim The contact zone of three zoogeographic realms, the Palearctic, Saharo-Arabian, and Oriental, is the evolutionary cradle of high species-richness and endemism in Iran. In this study, we use traditional clustering and newly developed, network-based methods to investigate the biogeographic regions of Lepidoptera species in Iran. Additionally, we attempt to provide a finer spatial resolution of the potential contact zones between these zoogeographic realms and investigate their faunal exchange in southwest Asia.

Location Southwest Asia

Taxa Lepidoptera

Methods Potential ranges of Lepidopteran species were estimated using species distribution modeling and masking suitable ecosystems based on the most comprehensive dataset available for the group in Iran. A presence/absence matrix was generated to cluster species assemblages using distance- and network-based methods. We used the optimal number of clusters optimal number of species assemblages to delineate the bioregions of Lepidoptera using distance- and network-based methods. We then explored the potential transition and contact zones between bioregions and zoogeographic realms for faunal exchanges in Iran and neighboring countries.

Results Despite small differences, the presence of five main bioregions for Lepidoptera was suggested by both distance- and network-based methods. Beyond this, six and seven small zones were detected by the network- and distance-based method, respectively, on the overlapping areas between major bioregions as potential transition zones.

Main conclusions The results of this study suggest a crucial transitional position of Iran between three main global zoogeographic realms. While similar to the results of distance-based methods, the bioregions detected by the network-based method are more compatible with previously identified ecoregions, macrobioclimates, and phytogeographical regions in the country. The detected regions on the edges of the main bioregions in the south of the country can be considered as contact zones of the Palearctic, Saharo-Arabian, and Oriental realms. However, further studies are needed to investigate the historical and ecological drivers that differentiate the species assemblages between bioregions and zoogeographic realms.

Keywords: Bioregionalization, contact zone, distance-based method, Geometridae, Lycaenidae, network-based method, zoogeographic realms, Zygaenidae.

Introduction

Biogeographic regions are distinct spatial units of species co-occurrence, which subdivide biomes into meaningful clusters of exclusive species assemblages (Olson et al., 2001; Carstensen et al., 2013; Antonelli, 2017; Edler et al., 2017; Ficetola et al., 2017). These units provide a great framework for understanding the historical evolution of habitats with their biological communities and associated environmental drivers (Harrison & Cornell, 2008; Carstensen et al., 2013; Antonelli, 2017; Ficetola et al., 2017). Hence, the concept of biogeographic regions plays an important role both in fundamental studies of biogeography and evolution and in practical studies, for which biodiversity conservation is a prime example (Olson et al., 2001; Kreft & Jetz, 2010; Bloomfield et al., 2018; Montalvo-Mancheno et al., 2020; Briega et al., 2023).

Although early works on bioregionalization were mainly subjective (Sclater, 1858; Wallace, 1876; Elton, 1946), different analytical approaches have been developed to define distinctive bioregions based on different criteria, e.g., species (dis)similarity (Kreft & Jetz, 2010; Carstensen et al., 2013; Vilhena & Antonelli,2015). The two main approaches currently used are distance- based (DM) and network-based (NM) clustering (Carstensen et al., 2013; Bloomfield et al., 2018; Edler et al., 2017). While DM cluster the bioregions according to the distance between the sites (e.g., grid cells, raster pixels) based on the (dis)similarity of contributed species in each site (Bloomfield et al., 2018), NM consider the correlation between species occurrence and studied sites (as two-mode or bipartite network), and consequently this method is able to identify and group together species and sites that are strongly interconnected (Carstensen et al., 2013; Vilhena & Antonelli, 2015). A comparison of the bioregionalization as estimated using both methods may help to define bioregions more objectively and explore the species composition of transition zones at the overlap of different biogeographic regions.

Transition zones are located where bioregions overlap along with shifts in biotic (species composition) and abiotic features (climate, geology, etc.; Morrone, 2004; Ferro & Morrone, 2014). These regions are characterized by complex species assemblages with different affinities (Halffter & Morrone, 2017; Morrone, 2023). The species assemblage of a transition zone is a result of evolutionary and ecological differentiation between affiliated bioregions (Halffter & Morrone, 2017; Morrone, 2023). Iran is located at the meeting point of three of global zoogeographic realms (Palearctic, Saharo-Arabian and Oriental; Holt et al., 2013; Ficetola et al., 2017; Fig. 1). The country is characterized by high landscape heterogeneity on the one hand, and steep climatic gradients on the other, which leads to a high habitat diversity and heterogeneity (Fig. 1). Moreover, the western and northern regions of the country are part of two biodiversity hotspots, the Irano-Anatolian and Caucasus (Mittermeier, 2000; Myers et al.,

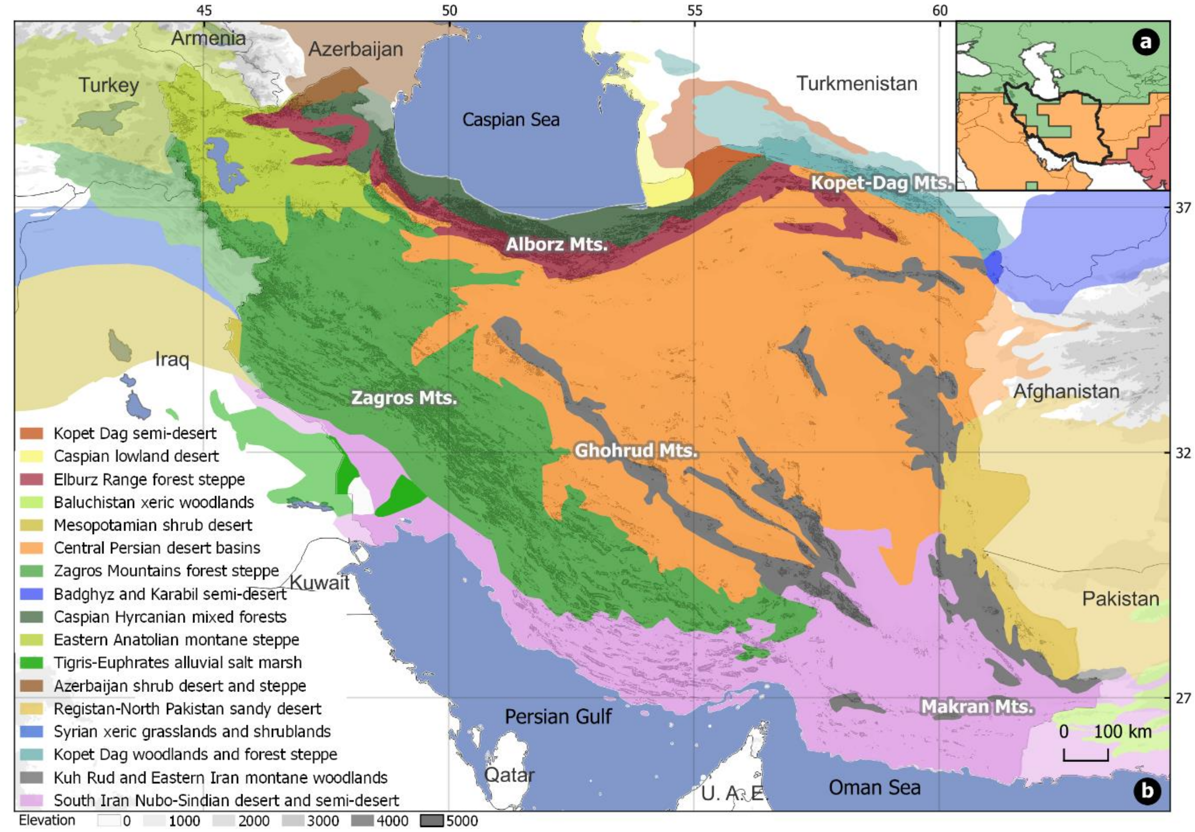

Figure 1. a) The map depicts the location of Iran in the southwest of Asia on the intersection between the three zoogeographic realms Palearctic (green), Saharo-Arabian (orang), and Oriental (red; Hot et al., 2013). b) A modification for identified ecoregions for the study area and neighboring countries by Dinerstein et al. (2017), with layers of elevation and topology, and the name of five main mountain ranges (Mts.).

2000). The landscape complexity and climate heterogeneity are reflected in the species composition of the fauna and flora (Noroozi et al., 2018; Rajaei et al., 2023a; Yusefi et al., 2019; Yousefi et al., 2023), pronouncing the importance of the country as a macro-scaled transition zone between different regions with an outstanding biodiversity (Yusefi et al., 2019; Yousefi et al., 2023). However, there is a significant deficiency in our knowledge regarding the biodiversity and distribution patterns of the majority of faunal groups in Iran.

Despite the high biodiversity and endemism in Iran (Noroozi et al., 2018; Rajaei et al., 2023a), there are only few studies investigating the biogeography of the species composition, particularly for invertebrates (Yusefi et al., 2019). Phytogeographical studies consistently subdivided the country into regions compatible with macro-bioclimatic regions (White & Léonard, 1991; Djamali et al., 2011). On the other hand, zoogeographic studies mainly focused on well-known species of vertebrates such as mammals (Blanford, 1876; Yusefi et al., 2019), birds (Zarudny, 1911; Scott et al., 1975), reptiles (Anderson, 1968), and fishes (Coad, 1985), which revealed different number of bioregions based on the studied groups. The bioregionalization studies of the arthropods are scant and have been limited only to a few families of Lepidoptera, ants and planthoppers (Naumann, 1987; Dubatolov & Zahiri, 2005; Matov et al., 2008; Paknia & Pfeiffer, 2011; Mozaffarian, 2013). These studies suggested a complex species composition, particularly in the southern regions. Nevertheless, additional studies based on larger datasets may provide a better portrait of the faunal complexity at contact zones of zoogeographic realms in the country. To do so, we investigate the bioregionalization of a recently cataloged order Lepidoptera in Iran (Rajaei et al., 2023b**)**, as one of the most diverse and species-rich insect groups with at least 4,812 confirmed species (Rajaei et al., 2023a) and over 9,000 total estimated species in the country (Landry et al. 2023).

In this study, we aim 1) to delineate bioregions within Iran based on the three best-studied Lepidoptera families (Geometridae, Lycaenidae and Zygaenidae). Apart from a well-known taxonomy, each of these three families has distinct bionomy, ecology, behavior and adaptation likely increasing the resolution of our results; 2) to investigate the importance of the country as macro-scaled transition zones by exploring the common faunal elements of bioregions in Iran and neighboring countries; and finally 3) to investigate the faunal exchange within the transition zones as potential contact zones between different major bioregions and zoogeographic realms.

Material and Methods

Occurrence dataset

In this study, we used the most comprehensive set of occurrence data for Iranian Lepidoptera species (Rajaei et al., 2023b). As the taxonomy and distribution patterns of most lepidoptera families in Iran are only fragmentarily understood, we focused only on three families (namely, Geometridae, Lycaenidae, Zygaenidae) based on following three criteria: i) taxonomically well-studied in the country; ii) high number of present species with occurrence data (in average more than ten records per species); iii) distinct ecology, biology, and distribution patterns in each family.

The family Lycaenidae (gossamer-winged butterflies) with 215 species is the largest Rhopalocera family in Iran (Nazari, 2003; Tshikolovets et al., 2014). On the other hand, we selected two of the best known families of non-Papilionoidea: Geometridae (geometer moths), with 539 species, which is the best known family of Macroheterocera in the country (e.g., Rajaei, 2012; Rajaei et al., 2012; Rajaei et al., 2013; Rajaei et al., 2022a; Rajaei et al., 2023b; Wanke et al., 2019; Wanke et al., 2020a; Wanke et al., 2020b), and Zygaenidae (burnet moths) with 73 species and an extremely high rate of endemism (46 %) in the country (e.g., Naumann et al., 1999; Keil, 2014; Hofmann & Tremewan, 2017, 2020a & b; Rajaei et al., 2023b). While Geometridae are nocturnal, Lycaenidae and Zygaenidae are active during the day (Hausmann, 2001; Hofmann & Tremewan, 2017).

All occurrences in our dataset were carefully georeferenced using the software Google Earth Pro v. 7.3.6.9345 (Table 1; Noori et al., 2023a; Rajaei & Karsholt, 2023). We gathered occurrences for 209 species of Lycaenidae, 515 species of Geometridae, and 73 species of Zygaenidae in the final dataset (Table 1).

Some species, particularly the endemic ones, were represented in the dataset with a few or even single records. To involve all species, we subdivided the species into two groups: *group-1* with more than ten records and *group-2* with less than 10 records. To generate comparable results for both groups in our analyses, some extra steps were taken as described below to generate potential species ranges.

Table 1. Structure of the dataset for selected families of the Lepidoptera in Iran. Min stands for minimum number of occurrences per species in the dataset, and Max depicts the maximum number of occurrences. Endemism shows the percentage of endemic species for each family.

Family	*Number of species*	*Number of records*				*Endemism*
		Records	***Min***	***Mean***	***Max***	
Lycaenidae	209	8587	1	41	532	28%
Geometridae	515	5279	1	10	164	21%
Zygaenidae	73	1164	1	16	68	50%

Species with SDM

To delineate the potential species ranges for *group-1*, first a minimum convex polygon was generated around the species' occurrences using the *mcp* function in the *adehabitatHR* package (Calenge, 2006) in the R (R Core Team, 2022). Since a delineated polygon can cover a wide range of ecosystems for each species, we accepted only those pixels of the *Terrestrial ecosystems map* (TEM) with confirmed species records within given ecosystems. TEM provides a fine-resolution map (250 m) of the ecosystems worldwide (Sayre et al., 2020) based on the similarity of climate, landform, and land cover. The results were saved as a raster file (in 'tif' format) representing the presence and absence of the species (pixel with values 1 and 0, respectively).

Additionally, to generate the potential range of a species in *group-1*, we used species distribution models (SDMs). This approach has been widely used to infer the species' geographical ranges (Elith & Leathwick, 2009; Elith et al., 2011; Fourcade at al., 2014). The Maximum Entropy (*MaxEnt*) algorithm was applied on the species with more than ten records to avoid overfitting in our prediction for a species potential range (Phillips & Dudík, 2008; Kreft & Jetz, 2010; Elith et al., 2011). We considered the sampling effort bias in our coordinate dataset by involving a bias layer for sampling intensity in *MaxEnt* following the methods described by Rinnan (2015; Phillips et al., 2009; Fourcade et al., 2014).

To predict the distribution of the species in the study area, we tested the correlation and contribution of the variables using pairwise Pearson's correlation coefficients ($r > 0.75$) and PCA (Principal Component Analysis; *ade4* package; Dray & Dufour, 2007) for 19 bioclimatic variables in the CHELSA dataset precipitation (Karger et al., 2017; for more details, see https://chelsa-climate.org). This dataset provides high-resolution climate raster (30 arc sec (WGS84)) for different parameters of temperature and precipitation. Finally, we chose three variables for temperature: 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), two variables for precipitation: bio13 (precipitation amount of the wettest month), and bio14 (precipitation amount of the driest month), and topology layer to consider the heterogeneity of the landscape in our modeling analysis. The topology variable was generated by applying the *terrain* function of the *raster* package (computing slope and aspect using default values) on the digital map for the elevation of the study area (Global Digital Elevation Model, ver. 3; www.nasa.gov).

We tuned the algorithm using an Akaike Criterion corrected for small sample size (AICc) approach as follows: the algorithm was repeated 10 times per species with varying combinations of feature classes and regularization parameters following the procedure described in Ginal et al. (2022). The optimal model settings with AUC_{test} (Area under the ROC Curve) higher than 0.7 and lowest AICc was selected to predict the potential range of the studied species based on random jackknife splits of the occurrence data of 80/20% and 100 replicates (Table 2, Appendix). As an environmental background, ecoregions within the *mcp* enclosing the species records were used and the projected potential distributions were restricted to this area. As presence-absence threshold, we used the average 10 percent training omission threshold across the 100 replicates. The accuracy of our predicted models was evaluated by assessing the multivariate environmental similarity surfaces (MESS), using the *mess* function from the *dismo* package (Elith et al., 2010). Consequently, to have a better presentation on similarity and dissimilarity of the occurrences data and climate space of the study area, we assigned value 1 to negative values of MESS and 0 to positive values.

Table 2. The average values for AICs and AUC, and contribution of selected environmental variables in SDMs for each studied family. The appendix provides the complete parametrization of MaxEnt and the average contribution of each environmental variable for each studied species.

Family	AICC	AUC (Train)	AUC (Test)	BIO5	BIO6	BIO7	BIO13	BIO14	Topology
Geometridae	403.12	0.80	0.79	10.84	18.29	21.33	16.79	16.37	15.89
Lycaenidae	747.27	0.80	0.77	17.25	11.43	14.39	19.48	22.99	14.18
Zygaenidae	341.38	0.81	0.78	19.53	13.16	12.55	18.79	16.55	18.77

Species without SDM

On the other hand, for species of *group-2* (less than ten occurrences) we generated a range based on the presence of the species within given ecosystems based on the *terrestrial ecosystems map* (TEM; Sayre et al., 2020) using *rangeBuilder* package (Rabosky et al., 2016). To consider the species with less than three records, we applied a different approach for species in *group-2*: the TEM was masked by a polygon around the species' occurrences with a buffer of 10 km. The results of this step were converted into raster files with presences value (1) for species in the study area comparable to the results of modeling the species' distributions in the previous step.

Presence/Absence Matrix (PAM)

In this step, the results of the species distribution range from both modeled species and masked species were concatenated in a raster file for all studied families, which was used for generating a species richness map and bioregionalization. To generate the PAM, the presence/absence raster layer of each species was added to a master raster layer using the *aggregate* function, first with 0.125° (= 450 arc sec ≈775 km^2) resolution to represent the presence/absence (1/0) of species. Then the abundance of species was calculated using an extra step by the *aggregate* function in a raster file with 0.5° (= 1800 arc sec ≈ 3100 km^2) resolution for each pixel (cell). The PAM was used to conduct distance-based (DM) and network-based (NM) bioregionalization. Likewise, we generated occurrence datasets from PAM and richness of species per cell (0.5°), which were used to conduct NM and an altitudinal density graph for the studied species (Supplementary Information (SI)). We also modeled the species richness per cell using a linear regression model (lm) embedded in the *ggplot 2* package to depict the correlation between elevation and topology of the study area for endemic and non-endemic species in each studied family (Fig. SI: S2, S4, S6).

Bioregionalization

The bioregionalization analyses were conducted for all selected families together and separately for each family (see SI). We concatenated PAMs for all studied families, Lycaenidae, Geometridae, and Zygaenidae, to generate a master PAM for bioregionalization analysis.

Distance-based bioregionalization

To cluster the grid cells of the study area, we generated a distance matrix based on the PAM using the *bioregion* package (Lenormand et al., 2023) in R. We used Simpson's dissimilarity between species assemblages of grid cells to determine the clusters (Kreft & Jetz, 2010). This metric is less sensitive to richness differences between the study units, which is useful for studying the compositional differences in species assemblages (Castro-Insua et al., 2018; Kreft & Jetz, 2010). To find the optimal number of clusters, we generated hierarchical trees for different numbers of cuts and simulated the clustering 100 times. Then, the optimum partitioning of the tree was evaluated using the *partition_metrics* function using the *pc_distance* method (Holt et al., 2013; Lenormand et al., 2023). Furthermore, the common species and indicator species of each bioregion were defined to compare the results with NM. Common species are defined as species that have a higher frequency (> 80 %) in the cells of a given bioregion. On the other hand, we selected the indicative species based on the higher-ranking score (> 20 %), which was calculated by the chance of finding a species in each bioregion compared with all other bioregions. Finally, we reported the 20 % of the highest rank score and 80 % of the highest abundance score as indicative and common species for each bioregion, respectively (Table 1).

Network-based bioregionalization

We clustered the distribution of the species using network-based community detection algorithms (*infomap*) embedded in the online interactive approach of *Infomap bioregion* (V. 2; Edler et al., 2017). We used occurrences generated from the potential species ranges generated by SDMs or by masking the TES in *Infomap bioregion* (Edler et al., 2017). Based on the occurrence of the species, a bipartite network was generated between the species' occurrence and the cells of the study area. This network was then clustered into a set of bioregions based on species assemblages. The *Infomap bioregion* application also reports the common and indicative species of each bioregion as defined above for DM. The application was tuned as follows: the size of the grid cells was considered as 0.5° to be comparable with the results of the DM. Since some species in our dataset occurred only in very small areas, we considered a minimum cell capacity of 1 and maximum by 300 to make it comparable to the results of the DM. The algorithm was repeated 100 times to reach an optimal consensus of the number of detected bioregions (Edler et al., 2017).

Results

The results of this study showed a strong convergence between the number of detected geographic units using distance-based (DM, with 12 units) and network-based methods (NM, with 11 units). Disregarding the small regions (with less than 12 cells), both methods yielded five main geographic units (hereafter bioregions) for the Lepidoptera species across Iran (the results for each family are provided in SI, separately). Here the main bioregions refer to those detected geographic units that together cover more than 90% of the study area. Furthermore, except for the detected regions in the northwest and across the Alborz (Elburz) Mountain Range (Mountain), there was high compatibility between two methods for the borders of detected regions in the other areas.

Higher species richness across the mountain ranges

As shown in Fig. 2, the species richness for all examined families had a positive correlation with mountainous areas, mainly across the main mountain ranges (Fig. 1). Although species of Lycaenidae and Geometridae had a wider elevational distribution range, the richness of Zygaenidae species was restricted to higher elevation regions of the Alborz, Zagros, and Ghohrud Mountain (Fig. 2). Our results revealed a strong correlation between species richness and higher elevation and topological heterogeneity (Fig. 2; see the SI for more details).

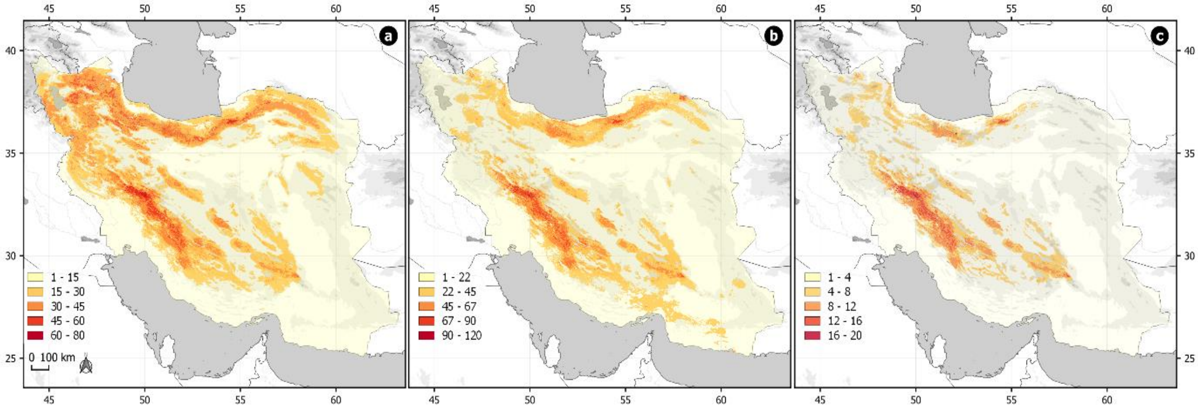

Figure 2. Species richness of studied families a) Lycaenidae, b) Geometridae, c) Zygaenidae in Iran.

Main detected bioregions

Here, we provide an overview of the main resulting bioregions across DM and NM according to the identified indicative species (the full results are provided in Table 3 and SI). For a better comparison between the resulting bioregions, we assigned a name to each according to the location of the bioregions (hereafter bioreg) of NM.

Alborz: One of main differences between NM and DM is the bioreg2 in NM, which is mainly extended from the South Caucasus region in the northwest of Iran toward the northeast across Alborz Mountain (Fig. 3). This bioregion has some overlap with bioreg2 and 5 of DM. However, none of the nine indicative species of bioreg2 by NM were the same as the indicative species of DM bioregions in the north and northwest (Table 3). Indicative species of bioreg2 of NM were shared with non-indicative species of bioreg1 of NM and bioreg1, 2, 5, and 6 of DM, e.g., *Cosmorhoe ocellata*, *Scotopteryx decolor* (Geometridae), *Aricia vandarbani* (Lycaenidae; Table 3).

Table 3. A comparison of bioregionalization results by distance-based (DM), and network-based (NM) methods. Table includes suggested name for the detected bioregions followed by corresponding regions ID by each method, and list of the most indicative species for each bioregion in different families of Lepidoptera Lycaenidae (Lcy), Geometridae (Geo), and Zygaenidae (Zyg). The endemic species are shown in bold.

Bioregion/ transition zone	***Detected bioregions***		***Most indicative species***	
	DM	NM	DM	NM
Alborz	5	1, 2, 8	*Polyommatus erotulus, P. zapvadi, Lycaena virgaureae* ^{Lyc}; *Lithostege witzenmanni, Stegania dilectaria,* ***Lithostege stadiei*** ^{Geo}; ***Zygaena christa***, ***Z. tenhagenova***, ***Z. mana*** ^{Zyg}	***Polyommatus peilei***, *P. marcid, P. luna, P. myrrhinus* $^{Lyc;}$ *Lithostege witzenmanni*, ***Scotopteryx decolor, Idaea wiltshirei*** ^{Geo}
Zagros	1, 5	1, 8	***Polyommatus Zarathustra***, ***Neolysandra fereiduna***, ***P. shahrami*** ^{Lyc}; ***Euphyia farsica***, ***Dicrognophos culminate***, *Kresnaia beschkovi* ^{Geo}; ***Rhagades tarmanni***, ***Z. naumanni***, ***Jordanita christinae*** ^{Zyg}	***Polyommatus peilei***, *P. antidolus*, *P. luna* ^{Lyc}; ***Idaea wiltshirei,*** *Kresnaia beschkovi* ^{Geo}; ***Zygaena mirzayansi, Z. naumanni*** ^{Zyg}
Central desert basins	2	3	***Plebejus ardashir***, ***Polyommatus eckweileri***, ***P. pseudoxerxes*** ^{Lyc}; *Hydrelia chionata*, *Eupithecia gueneata*, *Idaea deversaria* ^{Geo}; ***Zygaena fusca***, ***Zygaenoprocris efetovi***, ***Z. hofmanni*** ^{Zyg}	***Polyommatus baltazardi***, ***Plebejus ardashir***, ***P. kermansis*** ^{Lyc}; ***Rhodostrophia vahabzadehi***, ***Nychiodes mirzayansi*** ^{Geo}; ***Zygaenoprocris hasarani***, ***Zygaena aisha*** ^{Zyg}
Persian Gulf and the Oman Sea coasts	3	4	*Azanus ubaldus*, ***Polyommatus sephidarensis***, ^{Lyc}; ***Scopula gracilis***, *Hyperythra swinhoei*, ***Nebula saidabadi*** ^{Geo}; ***Zygaenoprocris duskei*** ^{Zyg}	*Azanus ubaldus, Anthene amarah* ^{Lyc}; ***Scopula lactarioides***, *Isturgia disputaria, Microloxia indecretata, Pseudosterrha paulula, Zamarada minimaria, Idaea mimetes, Gonodontis clelia* ^{Geo};
Kopet-Dag	4, 6, 7	5, 7	*Polyommatus dorylas,* ***P. tenhageni***, *P. phyllides* ^{Lyc}; ***Scotopteryx kurmanjiana***, *Eupithecia turkmena, Digrammia rippertaria* ^{Geo}*;* ***Zygaenoprocris khorassana, Z. fredi***, *Z. minna* ^{Zyg}	*Polyommatus tenhageni, Neolycaena tengstroemi, Turanana dushak* ^{Lyc}; *Cinglis eurata, Protorhoe turkmenaria, Stegania dalmataria* ^{Geo}; ***Zygaenoprocris khorassana***, ***Z. fredi***, ***Zygaena esseni*** ^{Zyg}
Central Zagros	1, 2, 3	6	***Scopula hoerhammeri, Idaea wiltshirei, Eupithecia mahomedana, E. brandti, E. sectile, E. cheituna, E. aduncata,*** *E. bastelbergeri, Eumera hoeferi* ^{Geo}	
Khuzestan plain	1, 3	10	*Phaiogramma polemia, Isturgia hopfferaria, Scopula relictata, Eupithecia ultimaria,* ***Pasiphila palaearctica,*** *Dicrognophos sartata* ^{Geo}	

Zagros: Bioreg1 of NM extends from the northwest of the country toward the southwest and central regions across Zagros Mountain (Fig. 3). This bioregion is mainly comparable with bioregion 1, and 5 of the DM. Bioreg5 of DM in the northwest of Iran shared some species with bioreg1 of NM, e.g., endemic species of Lycaenidae (e.g., *Polyommatus luna*, *P. aereus*). Additionally, bioreg8 of NM in the very northwest on the border with Turkey had some identical species with bioreg5 of DM (e.g., *P. myrrhinus, P. baytopi,* and endemic species: *P. urmiaensis* (Lycaenidae) and *Rhodostrophia calabra* (Geometridae)). Some endemic species, like *Zygaena mirzayansi* (Zygaenidae), and *Polyommatus peilei* (Lycaenidae) were indicative species for bioreg1 in both NM and DM methods.

Central desert basins: Bioreg3 in NM and bioreg2 in DM are extended across the central desert basins; some endemic species, such as *Plebejus ardashir*, *Polyommatus kermansis* (Lycaenidae), *Rhodostrophia vahabzadehi* (Geometridae), were among the indicative species of these bioregions (Fig. 3).

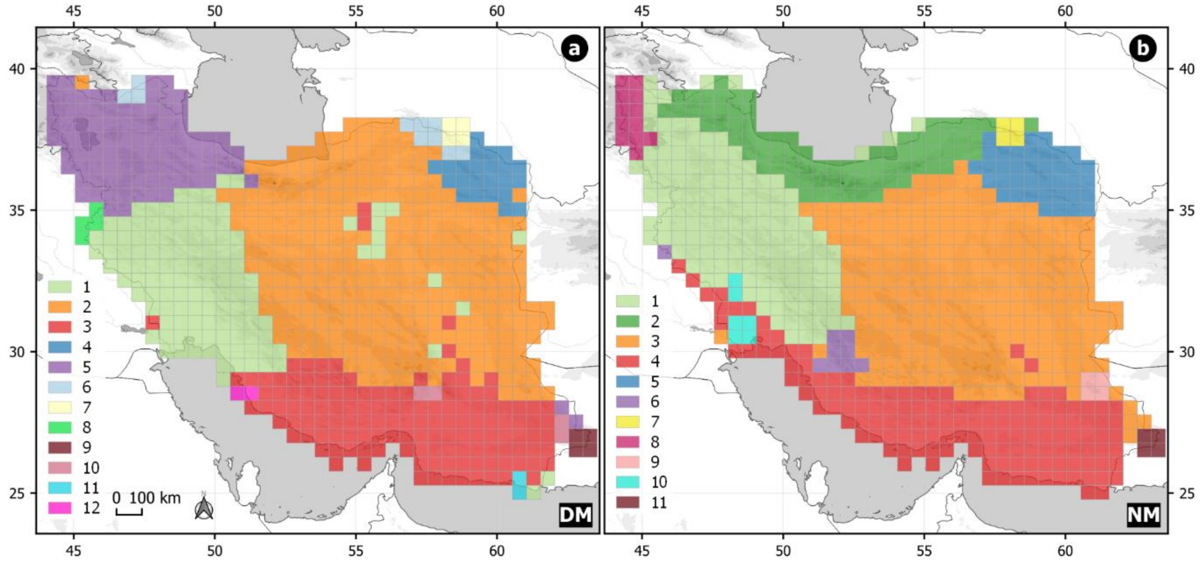

Figure 3. Bioregionalization of Iranian Lepidoptera based on the three families of Lycaenidae, Geometridae, and Zygaenidae using a) distance-based (DM) and b) network-based methods (NM).

Persian Gulf and the Oman Sea coasts: One of the distinctive bioregions in both methods was located across the northern seashores of the Persian Gulf and the Oman Sea (bioreg4 in NM and bioreg3 in DM). Bioreg4 in NM extended from the southwest of the country (Khuzestan province) towards Sistan-o-Baluchestan province in the southeast and shared a vast area with bioreg3 of DM (Fig.3). Endemic species, like *Scopula lactarioides* (Geometridae), and non-endemic species, such as *Azanus ubaldus*, *Anthene amarah* (Lycaenidae), *Isturgia disputaria*, and *Microloxia indecretata* (Geometridae) were listed as indicative species by both methods (Table 3).

Kopet-Dag: bioreg5 of NM and bioreg4 of DM delineated a distinct bioregion across the Kopet-Dag Mountain in the northeast. Endemic species, like *Polyommatus tenhageni* (Lycaenidae), *Zygaenoprocris fredi*, *Z. khorassana*, and *Zygaena esseni* (Zygaenidae), were among the most indicative species for both bioregions. Furthermore, some non-endemic species, such as *Cinglis eurata* (Geometridae), *Neolycaena tengstroemi* (Lycaenidae), *Zygaenoprocris albertii* (Zygaenidae), were indicative species of both bioregions (Fig.3, Table 3).

Transition zones

Besides the main bioregions, there were some small and distinct regions cover a few grid cells (Fig.3). Respectively, seven and six small regions were detected on the overlapping of the main bioregions by DM and NM. These regions (zones) contain between two to 12 cells within the study area, mainly on the borders of the country with neighboring countries. Zone6 and 7 from DM included some cells in the northeast and shared the most indicative species with zone7 of NM, e.g., *Stegania dalmataria*, *Phaselia narynaria*, *Protorhoe turkmenaria* etc. (Geometridae; Table 3). Zone6 of NM represented a transition between three bioregions 1, 3, and 4 of NM (Fig. 3). The most indicative species for this bioregion were *Scopula hoerhammeri*, *Idaea wiltshirei*, and *Eupithecia mahomedana* (Geometridae), which are shared with bioreg1 of DM. Zone10 of NM shared some indicative species with several bioregions of DM (e.g., *Phaiogramma polemia*, *Isturgia hopfferaria* with bioreg1, *Dicrognophos sartata* with bioreg1 and zone8, and *Pasiphila palaearctica* with bioreg3 (Table 3)). Moreover, there were some detected zones in the southeast (Sistan-o-Baluchestan province): zone9 in DM and zone11 in NM (Fig. 3). These zones were defined based on the two species *Tarucus alternatus* (Lycaenidae) and *Scopula ornata* (Geometridae) in NM and only by *Tarucus alternatus* in DM.

Discussion

The primary objective of the current study was to generate new knowledge on biogeographic regions of Lepidoptera in Iran as a macro-scaled transition zone between some of the diverse biogeographic regions in southwest Asia. Our analysis yielded five major bioregions for the Lepidoptera in the country based on the indicative and common species of the families Geometridae, Lycaenidae, and Zygaenidae (Fig. 3, Table 3; also see SI). Furthermore, we identified transition zones between these main bioregions across mountain ranges in the southern part of the central desert basins (Fig. 3), which at a regional scale might be considered as potential contact zones between zoogeographic realms within Iran.

High species richness within global biodiversity hotspots

The number of well-studied groups of Iranian Lepidoptera like Papilionoidea and Zygaenoidea is comparable with the European fauna (Landry et al., 2023; Rajaei et al., 2023a). For instance, so far, 469 species of Papilionoidea have been recorded for Iran (Rajaei et al., 2023b). In comparison 463 species are known across the Mediterranean biodiversity hotspot (Numa et al., 2016; Wiemers et al., 2018), with 98 species of butterflies being endemic (21%), mainly distributed in the mountainous areas in

North Africa, southern Europe, and Turkey (Numa et al., 2016). The rate of endemism for Papilionoidea of Iran is approximately 17% (79 species) which increases across the mountainous areas (Noori et al., 2023b; Rajaei et al., 2023a). In line with previous research, we observed a strong correlation between endemism and species richness, and regions with higher elevation and topological heterogeneity in Iran (Fig. 2; SI). Two out of the 36 global biodiversity hotspots extend in mountainous areas in the northern and western areas of the country, which mainly cover mountainous areas e.g., Zagros, Alborz, and Kopet-Dag Mountain ranges (Mountain; Mittermeier, 2000, Myers et al., 2000; Cañadas et al., 2014). Similar patterns have been found for the flora and fauna (Noroozi et al., 2018 & 2019; Yousefi et al., 2022). Globally, mountain ranges have been suggested as one of the main drivers for shaping current distribution of the species (Antonelli, 2017; Ficetola et al., 2017). The mountain ranges in Iran provide a wide range of microhabitats, likely representing glacial refugia, and act as a as barriers and corridors for the distribution of faunal elements across different zoogeographic realms (Rajaei Sh et al., 2013; Ghaedi et al., 2021; Yousefi et al., 2023).

Bioregions in Iran

We found a clear subpartitioning of the biodiversity of Lepidoptera within the country by bioregionalization methods. We detected five major bioregions, most of which were largely supported by both distance- (DM) and network-based (NM) methods (Fig. 3). Nonetheless, the outcomes of the NM provided a more comprehensive depiction of bioregionalization. Previous studies reported higher sensitivity for the NM compared with the DM in detecting bioregions (Vilhena & Antonelli, 2015; Bloomfield et al., 2018; Yusefi et al., 2019). Detected bioregions by NM roughly aligns with the previous studies on the regionalization of the fauna and flora in Iran (e.g., Blanford, 1876; Anderson, 1968; Zohary, 1973; White & Léonard, 1991; Yusefi et al., 2019; Fig.4). Most of the bioregionalization studies for the country were conducted using descriptive/qualitative approaches and in a few studies clustering methods were applied (Dubatolov and Zahiri, 2005; Matov et al.,2008). Yusefi et al. (2019) is the only comparable study which used both NM and DM to define bioregions of the mammals of Iran. They respectively identified seven and five bioregions using NM and DM for the country. Although there is a general similarity between detected bioregions of NM and DM by Yusefi et al. (2019) and identified bioregions in this study, our results depict several main differences particularly for bioregions in the northern regions. Similarly, Yusefi et al. (2019) reported better sensitivity for NM compared to DM. Furthermore, major detected bioregions by NM in our study are largely consistent with the identified ecoregions (Dinerstein et al. 2017) and bioclimatic regions (Djamali et al., 2011) for the country. Hence, it appeared that in comparison with DM, NM can better tackle the challenges in bioregionalization studies (Vilhena & Antonelli, 2015; Yusefi et al., 2019).

Affiliation of Bioregions in Iran

The major bioregions for Lepidoptera of Iran have affinities to different zoogeographic realms. Although most of the northern bioregions belong to the Palearctic, at a finer resolution, the species assemblages of the bioregions in the northwest of Iran mainly share species with the Caucasus, Transcaucasia, the north of Iraq, and eastern Turkey (Hofmann & Tremewan, 2017). According to our results, the detected Alborz bioregion ranged from the northwest of Iran to regions in the northeast through Alborz Mountain (Fig. 3 & 4). The Alborz Mountain draws a barrier for the distributions between temperate bioclimates on the seashores of the Caspian Sea and the dry and hot areas of the central desert basins, at the intersection between the Euro-Siberian and Irano-Turanian phytogeographic regions (Fig4.; White & Léonard, 1991; Zohary, 1973; Djamali et al., 2011). For instance, species like *Zygaena araxis*, *Z. lonicera*, *Satyrium ilicis*, *Lycaena tityrus*, *Nychiodes waltheri*, *Hydria hyrcana* etc. are distributed from Transcaucasia towards the most western part of Alborz Mountain (Tchikolovets et al., 2014; Hofmann & Tremewan, 2017; Wanke et al., 2020a; Stadie et al., 2022). Additionally, some species like *Zygaena filipendulae*, *Z. purpuralis*, *Z. monis*, *Z. brizae* (Zygaenidae); *Lycaena thetis, L. tityrus, Cupido minimus* (Lycaenidae) have their most southern and eastern distribution points across the Alborz Mountain or mountains of Azerbaijan in the northwest (Tshikolovets et al., 2014; Hofmann & Tremewan, 2020a, 2020b).

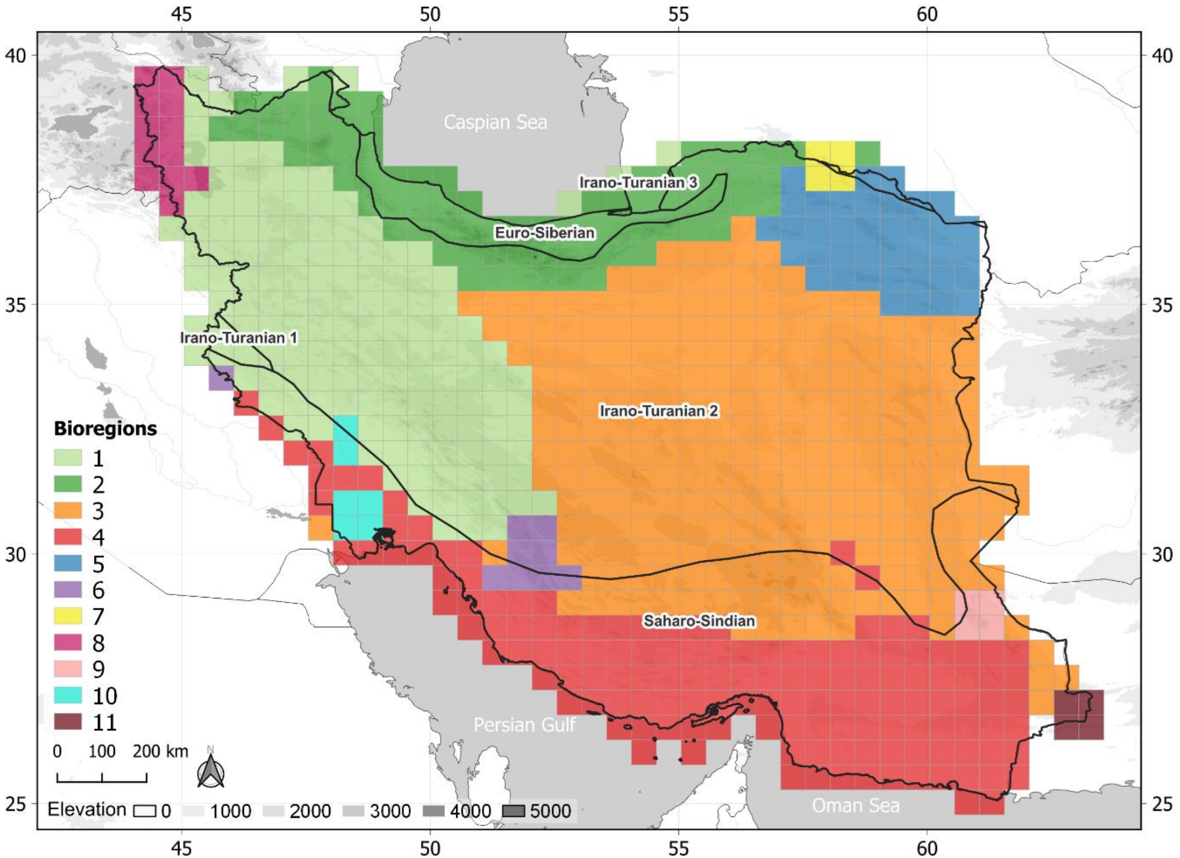

Figure 4. Spatial convergence of detected bioregions for Lepidoptera using network-based method with phytogeographical regions in Iran (modified map from White & Léonard, 1991).

Simultaneously, the Alborz Mountain acts as a corridor connecting the Lepidoptera fauna between Caucasus/Transcaucasia and Central Asia, e.g., *Lycaena phoenticurus*, *Satyrium spini, Callophrys rubi* (Lycaenidae), *Phaselia pithana*, and *Lithostege excelsata* (Geometridae; Rajaei et al., 2011; Tchikolovets et al., 2014; Werner et al., 2023). For instance, several species like *Zygaena turkmenica* (Zygaenidae), *Nychiodes divergaria*, *Euphyia frustata*, *Philereme transversata*, *Hydria hyrcana*, and *Rhodostrophia terrestraria* (Geometridae) are distributed from Turkey to Afghanistan through this mountain range (Rajaei, 2012; Hausmann et al., 2016; Stadie & Stadie, 2016; Stadie et al., 2022; Feizpour et al., 2018; Hofmann & Tremewan, 2020a; Rajaei et al., 2022b; Rajaei et al., 2022a). For the mammals of Iran, the areas across the Zagros, Alborz, and Kopet-Dag Mountain were detected as a distinct bioregion using the network-based method (Yusefi et al., 2019), while using the same method we detected three different bioregions in this area. Generally, the regions across the Alborz Mountain have been detected as a distinct bioregion for several taxa e.g., tiger moths (Dubatolov and Zahiri, 2005), ants (Paknia and Pfeiffer, 2011), planthoppers (Mozaffarian, 2013), and dragonflies (Schneider et al., 2018). Similarly, the Kopet-Dag Mountain in the northeast of Iran serves as a barrier between species assemblies of the central desert basins and central Asia fauna (Memariani, 2020; Yousefi et al., 2023). This region has already been suggested as a distinct bioregion for different taxa of e.g., flora (Memariani, 2020), lizards (Anderson, 1968) and tiger-moths (Dubatolov & Zahiri, 2005). However, this area was not detected as a distinct bioregion for mammals of Iran (Yusefi et al., 2019).

Climatologically the Zagros bioregion as detected in this study is compatible with Mediterranean continental regions in Iran (Djamali et al., 2011). In view of biodiversity, this region aligns with western Irano-Turanian phytogeographical provinces (White & Léonard, 1991), and Zagros woodlands for mammals (Blanford 1876). This bioregion is characterized by the presence of elements from the Transcaucasian and east Anatolian regions and a high rate of endemism for different taxa (Dubatolov & Zahiri, 2005; Mozaffarian, 2013; Hofmann & Tremewan, 2017). Furthermore, some species of Lepidoptera are distributed in the most extreme south of their ranges until the central and southern parts of Zagros Mountain e.g., *Lycaena asabinus, Thomares calimachus,* and *Ennomos quercaria* (Tshikolovets et al., 2014; Rajaei et al., 2023b).

In agreement with previous findings (e.g., Dubatolov & Zahiri, 2005; Ghaedi et al., 2021), it seems that the Zagros Mountain as well as the Ghohrud Mountain from the northwest towards the south of Iran, act as barriers affecting the distribution of the Palearctic and Saharo-Arabian elements (Fig. 3). Uplifting of the Zagros Mountain has been suggested as crucial factor in speciation and diversification of different taxa of vertebrates in the Iranian Plateau (e.g., Ahmadzadeh et al., 2017; Ghaedi et al., 2021; Yousefi et al., 2023). The western and southern slopes of the Zagros Mountain may represent a contact zone between the Palearctic and Saharo-Arabian zones, covering lowland and highland areas in the southwest and south of the country (Fig. 3; Dubatolov & Zahiri, 2005; Yusefi et al., 2019). The complexity of the species composition in this region supports this idea. The Zagros and Ghohrud Mountain, for instance, act as barriers for further dispersal of geometrid species like *Xanthorhoe wiltshirei* and *Pingasa lahayei*, and toward the south of Iran and for *Chazara briesis*, *Pieris ergane*, and *Turanana endymion* from Lycaenidae (Tshikolovets et al., 2014) towards central and northern regions of the country.

Potential contact zones of zoogeographic realms

The largest bioregion is found within the central desert basins (bioreg2 of DM and bioreg3 of NM), which has the longest border with all other major bioregions (Fig. 3a, b). By some differences, this region has been identified as a distinct bioregion for the other taxa, e.g., mammals (Yusefi et al., 2019), lizards (Anderson, 1968), ants (Paknia & Pfeiffer, 2011), and tiger-moths (Dubatolov & Zahiri, 2005). Theoretically, the central desert basins and the southern parts of the Zagros bioregion are the regions where the Palearctic region meets the Saharo-Arabian region in Iran (Holt et al., 2013; Ficetola et al., 2017). This collision can be seen at a finer resolution in two distinct small zones in the central Zagros (zone6) and the Khuzestan Plain (zone10 of NM), where a sudden shift between high elevation mountainous landscapes of the Zagros Mountain and lowlands in the north of the Persian Gulf occurs (Fig. 1 and 3). These two zones also were identified for the mammals of Iran as potential transition zones (Yusefi et al., 2019).

Besides the five major bioregions, we also detected small regions between main bioregions (zones Fig. 3b, Table 3). Some of these zones, particularly on the border with neighboring countries, might reflect misrepresentation because of the lack of entire species ranges in our analysis. However, those detected zones within the country can be considered as potential transition zones on the overlapping areas between main bioregions (Fig. 3b). By definition, a transition zone at any spatial level refers to the area of different overlapping bioregions with a sharp gradient in environmental features and species assemblage replacement (Morrone, 2004; Halffter & Morrone, 2017; Morrone, 2023). Therefore, detected small regions by NM in southwest of Iran zone6 (central Zagros) and zone10 (Khuzestan plain) probably represent the contact zone of the Palearctic and Sharo-Arabian zoogeographical realms (Fig. 3b; Table 3).

A corridor between Saharo-Arabian and Oriental regions

Climatologically, the Khuzestan Plain, and northern seashores of the Persian Gulf and Oman Sea belong to tropical macroclimate regions (Djamali et al., 2011). These regions have been suggested as a distinct ecoregion (Nubo-Sindiuan; Dinerstein et al. 2017; Fig. 1): a bioregion for the flora (Saharo-Sindian; Zohary, 1973; White & Léonard, 1991; Fig. 4), and a zoological subdivision for mammals (Mesopotamia and Persian Gulf shore; Blanford 1876), lizards (Anserson, 1986), ants (Paknia & Pfeiffer, 2011), and planthoppers (Mozaffarian, 2013). Species like *Anthene amarah,* with Saharo-Arabian affiliation, is distributed from South Africa through the Arabian Peninsula to the northern seashores of the Persian Gulf. Additionally, Oriental species like *Tarucus nara*, *Lachides ella* (Lycaenidae), *Traminda mundissima* (Geometridae), *Creatonotos gangis* (Erebidae) have the most western distribution in this region (Dubatolov & Zahiri, 2005; Tshikolovets et al., 2014; Rajaei et al., 2022b; Rajaeiet al., 2023b). The northern seashores of the Persian Gulf and Oman Sea serve as concurrent pathways, connecting species with Saharo-Arabian affiliation from Central Africa towards the northeast of Pakistan, India, and Sri Lanka, e.g., *Argina astrea* (Erebidae), *Tarucus rosaceus*, *Azanus ubaldus* (Lycaenidae), *Traminda mundissima*, *Problepsis cinerea*, *Scopula adelpharia*, and *Pseudosterrha paulula* (Geometridae; Dubatolov & Zahiri, 2005; Tshikolovets et al., 2014; Hausmann et al., 2016; Stadie & Stadie, 2016; Feizpour et al., 2018; Rajaei et al., 2022b).This is not limited to the invertebrates as in the case of mammals, the presence of Oriental elements such as the Asiatic black bear (*Ursus thibetanus*), the palm squirrel (*Funambulus pennanti*), and the Indian crested porcupine (*Hystrix indica*) have been documented at the southeastern-most corner of the country (Yusefi et al., 2019).

Conclusion

Here we provide the first study regarding bioregionalization of one of the most diverse orders of insects in Iran using distance and network-based methods. Our results emphasize the important role of topological and climatological factors in shaping the current biodiversity patterns at local and regional scales. Delineating bioregions for Lepidoptera of Iran are roughly in line with identified macroclimatic and phytogeographical regions (Fig. 4). While the identified bioregions generally align with bioregions of other vertebrates and invertebrates, there are certain discrepancies which could potentially be attributed to differences in physiology and habitat preferences. The results of this study, in line with previous studies on the biodiversity of the country, emphasize the crucial role of the country's mountains as barriers and corridors for shaping the biodiversity patterns in southwest Asia. The observed patterns suggest potential contact zones for three zoogeographic realms (Palearctic, Saharo-Arabian, and Oriental) at the northern seashores of the Persian Gulf and the Oman Sea. These contact zones provide excellent regions for further studies on historical, evolutionary, and ecological processes shaping the current biodiversity of southwest Asia. However, the main challenge of this study was the lack of data regarding the distribution of the targeted taxa in neighboring countries like Iraq, Turkey, Afghanistan, and Pakistan (Rajaei & Karsholt, 2023; Landry et al., 2023; Rajaei et al., 2023b). Although Lepidoptera Iranica provides a good dataset to generate a finer scale resolution picture of these contact zones, delineating the borders of Iran as a macro-scaled transition zone would require a better understanding on the distribution of the families in the neighboring countries. Considering the profound impacts of climate change in the Middle East and particularly southern regions in Iran (Segan et al., 2016; Hajat et al., 2023; Noori et al., 2023b), identified bioregions and transition zones in the current study can provide guidelines to determine protected areas with distinct evolutionary and ecological values.

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- Chapter V

Addressing the conservation gaps for Iranian Lepidoptera

Extensive mismatch between protected areas and biodiversity hotspots of Iranian Lepidoptera

Submitted in Insect Conservation and Diversity

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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 most 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 1,974 species from nine families of Lepidoptera, we delineated regions with statistically significant high diversity as biodiversity 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 the 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 centers, Macroheterocera, protected areas, Rhopalocera

Introduction

Insect populations are dramatically declining worldwide (Hallmann et al., 2017; Sánchez-Bayo, & Wyckhuys, 2019; Wagner, 2020; Blüthgen et al., 2023). 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, 2020). Protected area (PA) networks are expected to serve as bulwarks against the negative impacts of human-induced activities (Pringle, 2017; Maron et al., 2018; 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 (Nóbrega & De Marco, 2011; Verissimo et al., 2011; D'Amen et al., 2013; Dias-Silv et al., 2021; Chowdhury et al., 2022). 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 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 (Laurance et al., 2012; Visconti et al., 2019; Karimi & Jones, 2020). 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 require 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; Kati et al., 2004; Brooks et al., 2006; 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 (Myers et al., 2000; Mittermeier et al., 2011; Critical Ecosystem Partnership Fund, 2016). Defining these regions has been an attempt to provide a framework for concentrating conservation practices on higher-priority areas (Myers et al., 2000; Brooks et al., 2006; Mittermeier et al., 2011). 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 (Pressey et al., 1993; Ferrier et al., 2000; Brook et al., 2006;

Bacchetta et al., 2012; Le Saout et al., 2013; Cañadas et al., 2014; Noroozi et al., 2018). 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; Chandra & Idrisova, 2011; Joppa et al., 2013; Butchart et al., 2015; Farhadinia et al., 2022). Although there are substantial advances toward meeting these targets, most countries will likely not fulfill their commitments (Joppa et al., 2013; Watson et al. 2014; Farhadnia et al., 2022). 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 % (Farhadnia 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 (Visconti et al., 2019; Farhadnia et al., 2022).

In southwest Asia, two GBHs extend across the northern and western parts of Iran: the Irano-Anatolian and the Caucasus hotspots (Myers et al., 2000; Mittermeier et al., 2011; Critical Ecosystem Partnership Fund, 2016; Fig. 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 (Myers et al., 2000; Mittermeier et al., 2011). 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; Noroozi et al., 2018, & 2019; Yusefi et al., 2019; Noori et al., 2021; Yousefi et al., 2022; Yousefi et al., 2023). 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 (Noroozi et al., 2018, & 2019; Noori et al., 2021; 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 et & Shariati, 2017; Noroozi et al., 2019; Yusefi et al., 2019; Noori et al., 2021; Ludovicy et al., 2022; Yousefi et al., 2022). 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 4,812 species in this country (Rajaei & Karsholt, 2023; Rajaei et al., 2023a, 2023b; see Table 1). Landry et al. (2023) estimated that over 9,000 lepidopteran species in total may occur in Iran. The known species belong to 70 families with at least 892 endemic species (19.7 %; Rajaei et al., 2023a, 2023b). The rate of endemism among the well-studied families ranges from 9.4 % for Pieridae to 46 % for Zygaenidae to %(Table 1; Rajaei et al., 2023a). A preliminary analysis 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 et al., 2023a). 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.

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**	**39385**	**353 (18 %)**	**3728**

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.

Material and Methods

Study area

Globally, Iran is the eighteenth 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 km^2, 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 (Fig. 1). The heterogeneous topology of the terrestrial landscapes and sharp climate gradients provide 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 forest 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 & Karsholt, 2023; Rajaei et al., 2023b). 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 et al. (2023b) and the geographic coordinates of species records were carefully georeferenced using the software Google Earth Pro (v. 7.3.6.9345; Noori et al., 2023a). 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.

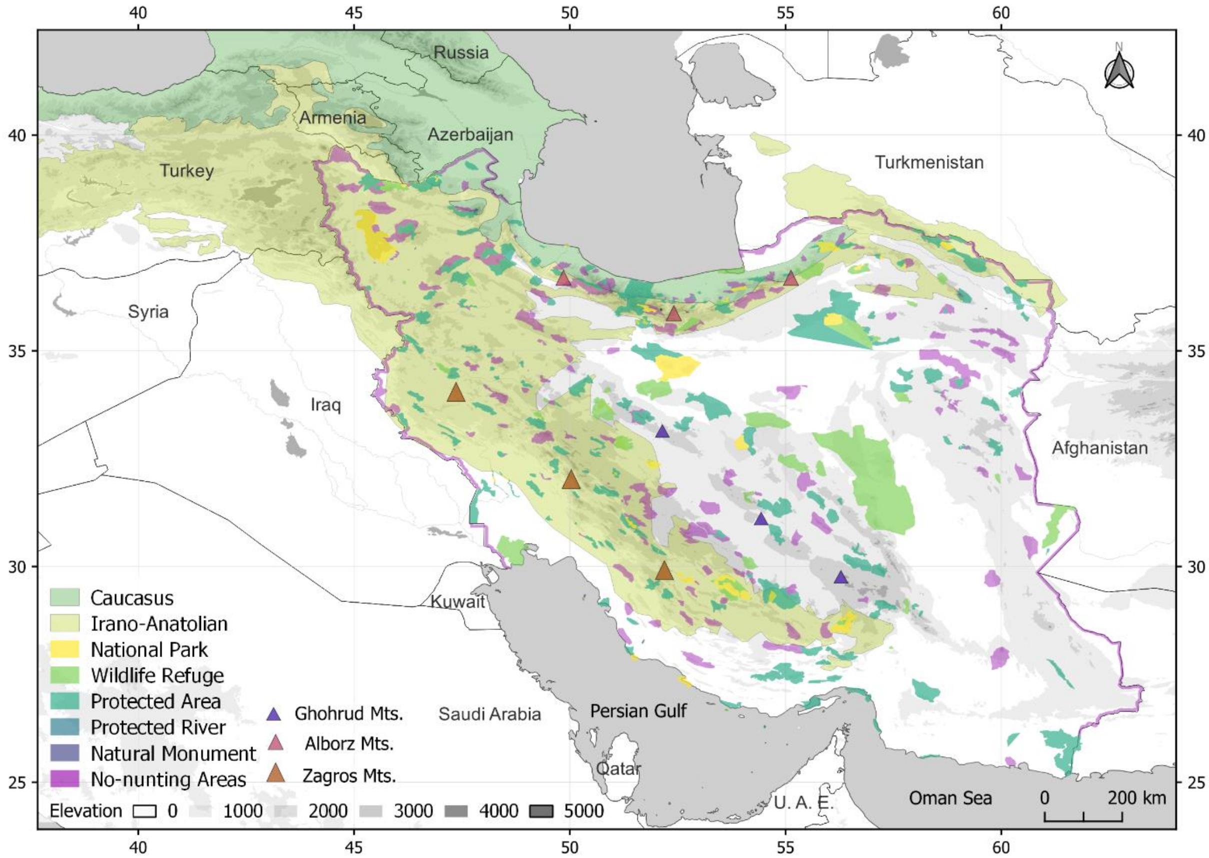

Figure 1. The map shows the location of Iran in the southwest Asia, with extension of two global biodiversity hotspots in the north and west: Caucasus, and Irano-Anatolian across two main mountain ranges Zagros and Alborz. The map indicates the distribution of different conservation areas (CAs) and no-hunting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

Data preparation

We endeavored 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, e.g., climate and land coverage (Sayre et al., 2020).

To mask 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 ten 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 ten occurrences. However, we employed a different strategy for species with fewer than ten 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; Phillips & Dudík, 2008; Kreft & Jetz, 2010; Elith et al., 2011). 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 ≥ 0.75) and PCA (Principal Component Analysis; *ade4* package; Dray & Dufour, 2007; see: Fig S1, supplementary Information (SI)). These abiotic factors included five 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, 2022). The density bias layer represents bias in sampling intensities per location towards the area which 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, 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 Criterion corrected for small sample size (AICc) approach (Morales et al., 2017; Ginal et al., 2022). To achieve this, the *MaxEnt* algorithm was executed ten 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. Appendix I 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 et al., 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 ten 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 3 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° to 1° (30 to 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°= 900 arc sec ≈ 650 km^2; r = 0.861), 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 on distribution patterns of centers of endemism for Iranian Lepidoptera (Myers et al., 2000; Crisp et al., 2001). Centers of endemism represent a geographical region characterizes by a high concentration of endemic species (Myers et al., 2000). Here, centers 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; Orme et al., 2005; Xu et al., 2017; Noroozi at al., 2019). ER index indicates the hotspots of the endemic species within a cell, which was measured by the sum of endemic species per cell (Fig. 2a). This method has been widely used to identify species-diverse regions (Crisp et al., 2001; Orme et al., 2005; Cañadas et al., 2014; Xu et al., 2017; Noroozi at al., 2019). 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 harboring 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 at al., 2019). Additionally, the area with highest species-diversity for all the studied species was mapped to compare the convergence with centers of endemism for the group within the country (Fig. 2b).

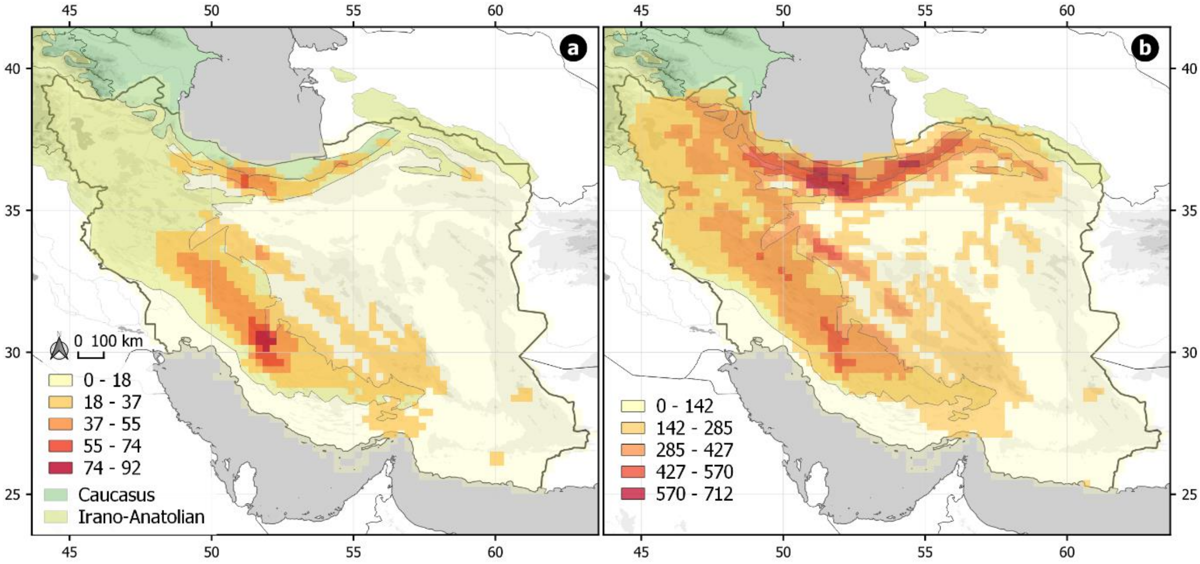

Figure 2. Richness of the endemic species (a) and all the studied species (b) of Lepidoptera at a resolution of 0.25°. The gray borders indicate the areas of two global biodiversity hotspots in Iran.

To define the centers of endemism, we used a hotspot analysis using Getis-Ord Gi* statistic (Gi*) by defining the cells which spatially harbor 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 which cluster as hotspots with statistically significant values (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 (Fig. 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 (Fig. 3a) and RRR and summing up the hotspot's values for each cell for both indexes (Fig. 3b). The priority hotspots' maps have four levels of hotspots, representing the areas with higher priority for conservation. In the priority hotspot map, higher values represent regions harboring both species-diverse regions of endemic and narrowly distributed endemic species (Fig. 4). Respectively, priority hotspots with the z-score of 4 (PH-4) to PH-1 represent areas with higher conservation priority for the Lepidoptera species in Iran (Fig. 4). The average species richness, number of grid cells and the areas of each hotspot of ER and RRR, and each PHs were assessed for further analyses. 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; Fig. 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 (Patial, 2021; Fig. S3 & S4)

Conservation gap analysis

We used the most updated polygon shapefiles for Protected Areas (PAs) (Iranian Department of Environment, 2023: https://en.doe.ir/; Fig. 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), Protected areas (Cat V; Dudley, 2008). In addition, no-hunting areas (NHAs) is an Iran-specific (unclassified by the IUCN) reserve type has been created in the 1990s, with the aim of population recovery of threatened species. No-hunting areas 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; Patial, 2021). Appendix 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).

Table 2. Description of all IUCN classified Iranian protected areas (PAs) in Iran, including no-hunting areas (NHAs; unclassified by the IUCN). 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 shows the sum up of the coverage for both PAs and NHAs and protected depicts only coverage of PAs.

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**

Table 3. Areas and conservation status of Iranian Lepidoptera's biodiversity hotspots. 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. * Covered values refer to the coverage rate of both PAs and NHAs and protected values indicate the coverage of PAs across hotspots and PHs.

Hotspots	Level	Species richness (mean)	Number of cells	Area (km^2)	In Iran (%)	Covered* (%)	Protected* (%)
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

Results

Endemic richness vs. total richness

Species-diverse regions for endemic species of Iranian Lepidoptera are mainly distributed within the two global biodiversity hotspots (GBHs); Irano-Anatolian and Caucasus (Fig. 1 & 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 (Fig. 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 harbor only a small share of Lepidoptera species and endemic taxa (Fig. 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 (Fig. 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 (Fig. 3). Overall, most of the detected hotspots are along the main mountain ranges Zagros and Alborz and consequently fall within two Global biodiversity hotspots. Although detected hotspots of ER and RRR cover a small proportion of the country (≈ 21 % and 9 %, respectively), they harbor 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 (Fig. 3a). This hotspot consisted of cells with 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 harbors a significant number of species with restricted distribution (median = 20, max = 47; Table 3).

In line with detected hotspots for ER and RRR indexes, priority hotspots (PHs) are mainly restricted to Zagros and Alborz Mountains (Fig. 4). As depicted in Fig. 4, the PHs (PH-4 & 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 harbors 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) harbor statistically significant ($p < 0.05$) more species richness for endemic Iranian Lepidoptera, in comparison with insignificant/coldspots regions (Fig. S3).

Conservation gaps

Currently, the terrestrial territory of Iran is covered by 17.25 % of protected areas (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 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; Fig. 4 & 5; Table 3). Protected areas (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; Fig. 1), whereas other categories of PAs collectively cover 4.98 % of the terrestrial area within the country: Wildlife refugia (Cat. IV) with 3.67 %, National parks (Cat. II) 1.25 %, Natural Monuments (Cat. III) 0.02 %, protected river (Cat. V) 0.04 % (Table 3).

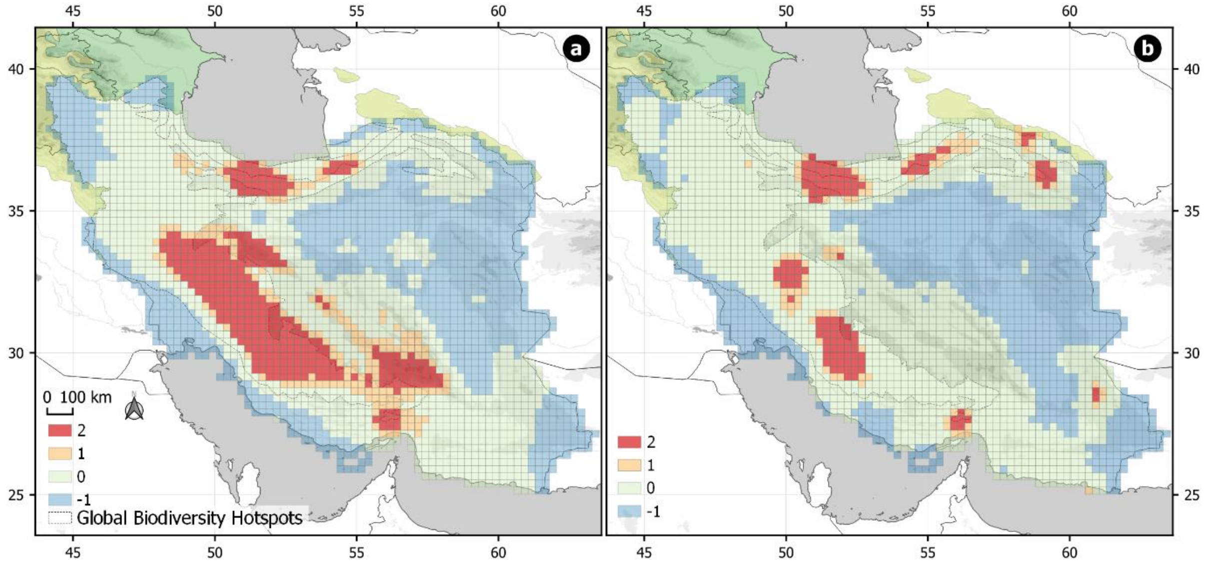

Figure 3. The detected biodiversity hotspots for two biodiversity indexes regarding richness of endemic species (ER; a) anc Range-rarity endemic species (RRR; b) of Iranian Lepidoptera. Hotspots with z-score 2 refer to cells which harbor highest richness of endemic species ($p < 0.01$) and hotspots with z-score 1 indicate cells with highest richness ($p < 0.05$).

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 (Fig. 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 (Fig. 4). Finally, our result indicated that different levels of PHs for Iranian Lepidoptera are only covered by approximately 25 % of the network of CAs (Fig. 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 ($p < 0.05$; Fig. S4).

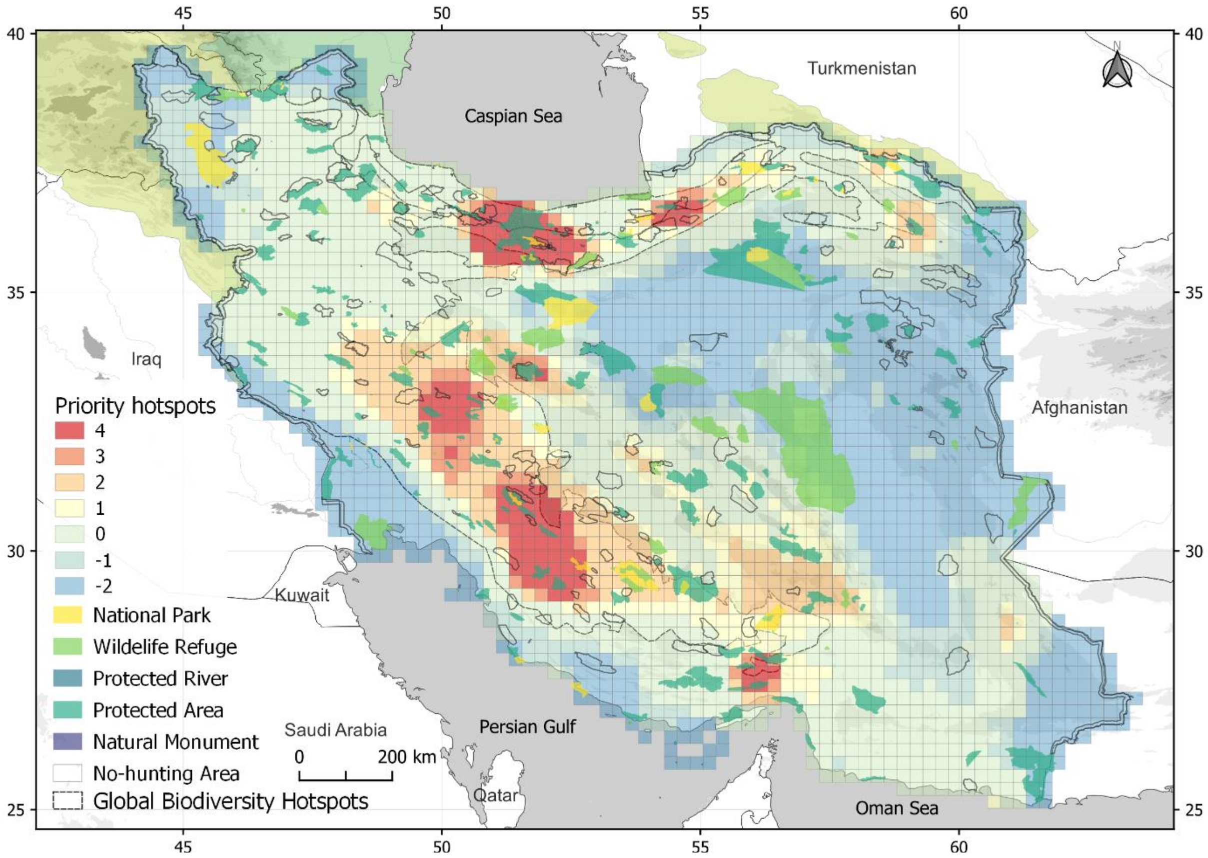

Figure 4. Coverage of the network of conservation areas (CAs) and no-hunting areas (NHAs) across different levels of Priority Hotspots (PHs) for Lepidoptera in Iran. The PHs indicated the overlapping cell with highest conservation probability for all endemic species (ER) and range restricted species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

Discussion

Hotspot within global hotspots

Lepidoptera of Iran are predominantly distributed across mountainous areas in the north and west of the country (Fig. 2; Keil, 2014; Tshikolovets et al., 2014; Hofmann & Tremewan, 2017; Rajaei et al., 2023b; Noori at al. 2023b). However, there is marginal convergence between the species-diverse regions of all the studied species and our detected biodiversity hotspots (hotspots) and priority hotspots for conservation (PHs) of endemic species (Fig. 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 (Fig. 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 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 (Fig. 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 neighboring 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 (Tshikolovetset al., 2014; Hofmann & Tremewan, 2017). 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 (Rajaei Sh et al., 2013; Ghaedi et al., 2021; 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; Rahbek et al., 2019; Perrigo et al., 2020). Higher topological heterogeneity of mountainous areas simultaneously provides centers 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 (Fig. 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; Rahbek et al., 2019; Qian et al., 2023). Although detected hotspots and PHs of Iranian Lepidoptera are highly congruent and cover a small proportion of the country, they harbor a high number of endemic and non-endemic species of Lepidoptera (Fig. 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 (Fig. 4). Our results revealed that only in the Central Alborz Mountains these PHs are protected by one fourth of their areas (Fig. 4). However, in the Central Zagros Mountains or eastern Alborz Mountains, PH-4 and 3 are only marginally protected by protected areas (PAs) or covered by PAs and no hunting areas (NHAs; Fig. 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, Fig. S3). However, these PHs have been protected only by 17 % and 10 % of their areas, respectively (Fig. 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 protected areas 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 et & Shariati, 2017; Noroozi et al., 2018 & 2019; Yusefi et al., 2019; Noori et al., 2021; Yousefi et al., 2022; Yousefi et al., 2023). In concordance with previous studies, our results revealed an extensive mismatch between the species-diverse regions of Lepidoptera and the current network of PAs (Fig. 4 & 5; Table 3). The detected hotspots and PHs of Lepidoptera mainly fall within two global biodiversity hotspots (GBHs), particularly the Irano-Anatolian hotspot (Fig. 2 & 4). In

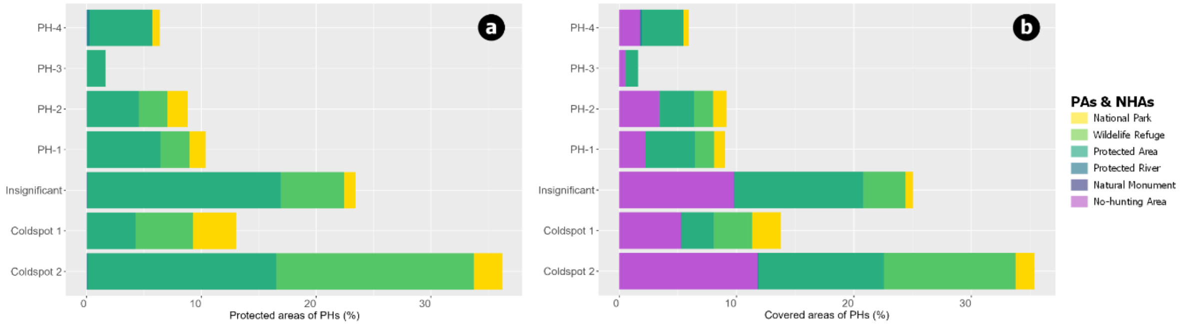

Figure 5. The stacked bar chart indicates the percent of protected (by PAs; a) and covered (by both PAs and NHAs; b) areas of each priority hotspots (PHs) for Iranian Lepidoptera. As shown, almost 75% of PAs and NAHs are covered non-priority areas and the different levels priority areas for endemic species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

general, the regions in the northern and western of Iran, across two major mountain regions of Zagros and Alborz, harbor most of the diversity for different taxa of fauna and flora (Noroozi et al., 2018, 2019; Yusefi et al., 2019; Noori et al., 2021; Yousefi et al., 2022; Yousefi et al., 2023), including Lepidoptera (Rajaei et al., 2023b). 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; Fig. 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 (Venter et al., 2017; Chowdhury et al., 2022). Since the 1950s, there has been a sporadic increase in the number and size of the PAs in Iran (Kolahi et al., 2012; Jowkar et al., 2016). 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 (Fig. 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 (Fig. 4 & S4). Hence, our result suggests the misplacement of PAs in the country toward 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 %; Chandra & Idrisova, 2011; Joppa et al., 2013; Butchart et al., 2015; Farhadinia et al., 2022; UNEP-WCMC & IUCN, 2023). On the other hand, no-hunting areas solely cover approximately 6 % (≈ 10,000 km^2) of the country, which is slightly smaller than protected areas (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 (Fig. 4). Therefore, these areas can be upgraded to higher management level for conservation of hotspots and PHs of biodiversity in Iran.

Protected areas under anthropogenic pressure

Protected areas provide a bulwark to conserve biodiversity and ecosystems with higher ecological values in an effective way (Brooks et al., 2004; Watson et al., 2014; Pringle, 2017). The current network of the PAs in Iran is not immune from anthropogenic effects including, 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 (Fig. 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 et al., 2023b) 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 centers 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 insect conservation has been ignored so far (Farashi et & Shariati, 2017; Noroozi et al., 2019; Yusefi et al., 2019; Noori et al., 2021; Chowdhury et al., 2022; Yousefi et al., 2022; Yousefi et al., 2023). Lack of financial and human resources, mismanagement, human encroachment, and lack of public awareness are among the main challenges PAs face in Iran (Kolahi et al., 2012; Jowkar et al., 2016). The results of this study indicate an obvious misplacement of PAs towards unpopulated and unfertile regions (Fig. 4). Given the importance of insects in all terrestrial and aquatic ecosystems, policy makers 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 centers 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 harbor the highest species richness of all studied Lepidoptera species (Fig. 2&4). Moreover, our identified hotspots and priority hotspots 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 not only conservation 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 by encompassing biodiversity across all three levels: species, ecosystems, and genetic diversity (Pressey et al., 1993; Kati et al., 2004).

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 centers 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 global biodiversity hotspots within the country, while these areas harbor 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 no-hunting areas (unclassified by the IUCN) has the potential to be upgraded to higher ranked IUCN protected area 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 protected areas 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 diminish the human-induced threats and climate change.

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- Chapter VI

Lepidoptera under Peril

A window to the future: effects of climate change on the distribution patterns of Iranian Zygaenidae and their host plants

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Abstract

Climate change has been suggested as an important human-induced driver for the ongoing sixth mass extinction. As a common response to climate change, and particularly global warming, species move toward higher latitudes or shift uphill. Furthermore, rapid climate change impacts the biotic interactions of species, particularly in the case of Zygaenid moths which exhibit high specialization in both habitat and host plant preferences. Iranian Zygaenidae are relatively well-known and represent a unique fauna with a high endemism rate (46%) in the whole Palearctic; as such they are a good model species to study the impact of climate change on future distributions. In this study, we used species distribution models (SDMs) and ensembles of small models (ESMs) to investigate the impact of climate change on the future distribution of endemic and non-endemic species of zygaenids, as well as their larval host plants. Three different climate scenarios were applied to forecast the probable responses of the species to different climate change intensities. Our results suggest that the central and southern parts of the country will be impacted profoundly by climate change compared to the northern regions. Beyond this, most endemic species will experience an altitudinal shift from their current range, while non-endemic species may move towards higher latitudes. Considering that the regions with higher diversity of zygaenids are limited to mountainous areas, mainly within the Irano-Anatolian biodiversity hotspot, the identification of their local high diversity regions for conservation practices has a high priority.

Keywords: Zygaeninae, Procridinae, poleward movements, altitudinal shifts, Species distribution modeling, Ensemble Small Models.

Introduction

Alongside habitat degradation and overexploitation, human-induced climate change has been considered one of the main drivers of the sixth mass extinction, which increased the rate of extinction by 100 times compared to the last five mass extinctions (Maxwell et al. 2016; Pimm et al. 2014; Shivanna 2020). Even optimistic scenarios for future climate change anticipate an increase in temperature, the concentration of CO2, and greenhouse gasses in the near future (Bellard et al. 2012; IPCC 2020; Ripple et al. 2020). It has been well documented that species commonly respond to climate change through changes in morphology, behavior, phenology, and geographical range shifts (e.g. Bellard et al. 2012; Della Rocca & Milanesi 2022; Howard et al. 2023; Rödder et al. 2021). However, pieces of evidence demonstrate that this response can vary among species (Parmesan & Gary Yohe 2003; Weiskopf et al. 2020). Different studies showed that the response of most taxonomic groups to climate warming is an altitudinal and latitudinal retreat (e.g. Biella et al. 2017; Dieker et al. 2011; Hickling et al. 2006; Parmesan & Gary Yohe 2003; Rödder et al. 2021; Thomas 2010). Undoubtedly, the species with narrower distribution ranges and strong reliance on host plants will be significantly more severe impacted compared to generalists (Bellard et al. 2012; Biella et al. 2017; Hoffmann et al. 2019; Mori et al. 2018; Thomas 2010).

The presence/absence of a species in a certain geographical and ecological space reflects a nexus between abiotic and biotic factors on the one hand and area(s) that species historically have been able to occupy on the other hand (Antonelli 2017; Brown & Carnaval 2019). The potential niche of a species is a geographical intersection between favorable abiotic (A) and biotic (B) factors for the species (Machado-Stredel et al. 2021; Milanesi et al. 2022; Soberón and Peterson 2005). However, due to some factors like dispersal ability, competition, and natural barriers, species would be able to occupy only some parts of the potential niche, named accessible area (Della Rocca & Milanesi 2020; Machado-Stredel et al. 2021). Therefore, any change in the abiotic and biotic factors can impact the habitat suitability of the species and consequently result in geographical shifts in the species range, particularly regarding endemic and rare species with narrow distributions (Bellard et al. 2012; Della Rocca & Milanesi 2020). Furthermore, species that rely heavily on specific interactions with other species, such as zygaenid moths, may be more vulnerable to these changes compared to generalist species.

Species of the family Zygaenidae, particularly endemic ones, spend the majority of their developmental time on a few plant species of the same genus or family (Hofmann & Tremewan 1996: Naumann et al. 1999). Two zygaenid subfamilies, the Zygaeninae and Procridinae, are mainly distributed across the Palearctic and their species can usually be found in open biotopes, areas exposed to the sun and light forests (Naumann et al. 1999). Although some species have a wide distribution range (across the whole Palearctic), most zygaenids have a regional or local distribution, and are extremely restricted to a few adjacent sites or are even unilocal (Hofmann & Tremewan 2017). Their larvae are mono- or oligophagous, their occurrence therefore strongly dependent on their host plant (Naumann et al. 1999). Consequently, future climate change can have a double effect on biodiversity, either directly by changing the habitat suitability of the species, or indirectly by affecting their interactions with their host plants.

With more than 46% of endemism, Iran is a unique hotspot for Zygaenidae diversity across the entire Palearctic (Hofmann & Tremewan 2017; Rajaei et al. 2023a). Iran is characterized by high landscape heterogeneity and a steep climatic gradient and it has been suggested as a transitional zoogeographical region between Palearctic, Oriental, and Saharo-Arabian realms (Holt et al. 2013; Rueda et al. 2013; Yusefi et al. 2021; Fig. 1). Several mountain ranges surround the high-elevation plateau of the country in the southwest of Asia (e.g., Zagros, Alborz, Kopet-Dagh), which provide a wide range of habitat for its biodiversity. Up to now, 73 species of the family Zygaenidae are known from the country, sorted in two subfamilies: Procridinae with 32 species and Zygaeninae with 41 species (Keil 2014; Rajaei et al. 2023a). The Iranian Zygaenidae are one of the best studied groups of non-Papilionoid, particularly over the past 50 years mainly by European zygaenologists (Rajaei et al. 2023b). Most of the species of this family are distributed across the mountainous areas in the north and west of the country, along two

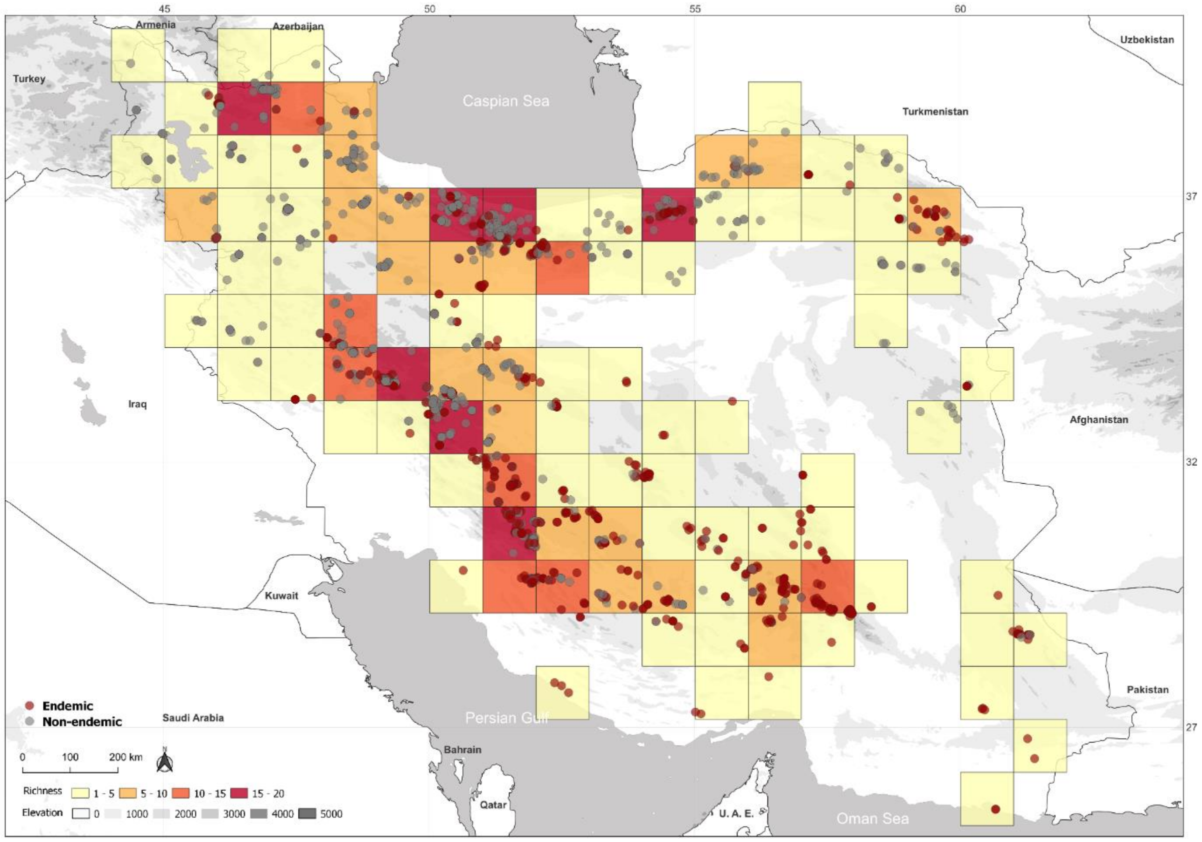

Figure 1. Species richness of Iranian Zygaenidae. The map shows the distribution of endemic species (red dots), and non-endemic species (gray dots) occurrences across the country at 1-degree geographical unit (≈ 12400 km2).

main mountain ranges (Mountain), Zagros and Alborz (Keil 2014; Rajaei et al. 2023a). These mountain ranges have historically served as barriers and corridors for gene flow and provided many species with microhabitats and glacial refugia (Ghaedi et al. 2021;

Noroozi et al. 2018; Sanmartín 2003). Distribution analyses confirmed that 86% of all the Zygaenidae species are distributed across these two mountain ranges (Hofmann & Tremewan 2017; Keil, 2014). Furthermore, more than 60% of the endemic species have been recorded in the Zagros Mountain and especially the central regions of this mountain range (Hofmann & Tremewan 2017; Keil, 2014). Besides these mountain ranges, isolated mountains on the sidelines of the central basin provide suitable habitats for several endemic species (e.g. Hofmann & Tremewan 2017; Keil 2014).

Despite the long-term study of the biology and ecology of Zygaenidae species in Iran, there is a big knowledge gap concerning their taxonomy, ecology, distribution patterns, and their conservation status. Therefore, in this study, we aim to 1) shed light on the ecology and the species distribution patterns of endemic and non-endemic species of Zygaenidae and their host plants across Iran. 2) Explore potential habitat change in response to climatic changes for endemic and non-endemic species of Zygaenidae using the simulated distribution of species and their host plants under different optimistic and pessimistic climatic scenarios at the end of the current century. To achieve our objectives, we used the most comprehensive existing dataset for the group. We expect that narrowly distributed species suffer more from climate change and particularly global warming than widely distributed, non-endemic species. The outcomes of our study would provide a resource for directing conservation practices toward areas with high priority for conservation under future climate change.

Material and Methods

Study area

Iran is the 17th largest country worldwide and is located in southwestern Asia between 25- 40° north and 44-64° east (Fig. 1). The country spans across three different macrobioclimatic regions: the Mediterranean (in center and north), the Tropical (in south), and a small part of the Euro-Siberian regions (along the southern coastline of the Caspian Sea; Djamali et al. 2011). In general, the climate of Iran can be considered arid to semi-arid with low annual precipitation (~ 250 mm; Ghasemi & Khalili 2008; Madani 2014). There is a steep gradient of temperature depending on the location between -3 to 7° C in the coldest month to 29 to 37° C for the warmest month (https://www.irimo.ir/en/climate).

Occurrence data

The checklist of the Zygaenidae of Iran includes the genera *Rhagades* (2 species), *Zygaenoprocris* (17 species), *Adscita* (one), *Jordanita* (12 species) and *Zygaena* (41 species; Rajaei et al. 2023a). To generate the dataset of occurrence data for all the Zygaenidae species, all data was gathered in a comprehensive literature review (e.g., Hofmann & Tremewan 2017, 2020a, 2020b; Keil 2014; Fig. 1). Additionally, Axel Hofmann provided additional occurrence data for distribution of the endemic and non-endemic species of Zygaenidae worldwide. The locations of all collected occurrences were carefully georeferenced using the software Google Earth Pro (v. 7.3.6.9345; Noori et al. 2023). The final dataset covered all 73 species of the family including more 2500 occurrences, of which 1710 records remained after removing duplicated and missing values (with minimum 1, mean 23, and maximum 117 records per species).

For this study, we selected 18 species (Table 1), from which 12 are endemic to Iran and the remaining are widely distributed in Central Asia, the Middle East, and the Palearctic. The species were selected if a) there were more than 10 records for the species in our dataset. b) The host plant(s) of the species is known, and we were able to gather more than 20 occurrence data for the host plant. c) The biology of species is well-documented to test the factor of feeding mode (seven species are monophagous, and the remaining 11 species are oligophagous). Furthermore, we used the dataset of the host plants of the examined species, including 10 plant species of the families Apiaceae, Fabaceae, Polygonaceae, and Rosaceae. Two out of these 10 species are endemic to Iran (namely: *Prunus eburnea* and *Ferulago carduchorum*; see Table 1). The coordinate dataset host plants were gathered from different published datasets, i.e. Flora Iranica (Rechinger 1963–2015), Revision of genus *Eryngium* (Wörz 2011), and GBIF database (Global Biodiversity Information Facility; www.gbif.org; the list of host plants and number of records is provided in Table 1; see the reference for occurrence dataset of host plants from GBIF: Table S1). The dataset includes occurrence data for species of host plant across their ranges worldwide.

Environmental variables

We obtained climate variables from the CHELSA dataset (Climatologies at high resolution for the earth's land surface areas, version 2.1) for both presence (1981–2010) and future (2071–2100; https://chelsa-climate.org). The dataset includes high-resolution raster files with a spatial resolution of 30 arc sec (WGS84) of downscaled model outputs for different parameters of temperature and precipitation globally (Karger et al. 2017). The future variables of the CHELSA dataset include three out of five simulated socio-economic scenarios of CMIP6 (the international Coupled Model Intercomparison Project 6) at roughly 1 km resolution from the National Oceanic and Atmospheric Administration (from GFDL-ESM4 model; Karger et al. 2017). These scenarios (hereafter: climate scenarios) have been modeled based on increases in temperature and the concentration of CO_2 and greenhouse gases such as methane (Table 2; Karger et al. 2017). Table 2 shows a short description of the climate scenarios we applied in this study (Spp126, Spp370, and Spp585; for more details, see https://chelsa-climate.org).

Table 1. List of the examined Zygaenidae species and their host plants, with endemism status and number of occurrences for both moth and its host plants after omitting duplicated, missing values, and thinning the coordinate dataset

Zygaenid species	**Host plant(s) in iran (family)**	**Endemism**	**Number of records**	
			moth	Host plant
***Rhagades brandti* (alberti, 1938)**	*Prunus eburnea* (Spach) Aitch. (Rosaceae)	Endemic	29	39
***Zygaena aisha* naumann & naumann, 1980**	*Ferulago carduchorum* Boiss and Hausskn (Apiaceae)	Endemic	10	34
***Zygaena araxis* koch, 1936**	*Bupleurum exaltatum* M. Bieb. (Apiaceae)	Non-endemic	34	422
***Zygaena cuvieri* boisduval, [1828]**	*Eryngium billardieri* F.Delaroche (Apiaceae)	Non-endemic	50	335
***Zygaena ecki* christoph, 1882**	*Onobrychis cornuta* (L.) Desv. (Fabaceae)	Endemic	20	316
***Zygaena fredi* reiss, 1938**	*Bupleurum exaltatum;* *Semenovia tragioides* (Boiss.) Manden. (Apiaceae)	Endemic	88	422; 24
***Zygaena ginnereissi* hofmann, 2000**	*Eryngium billardieri* (Apiaceae)	Endemic	10	335
***Zygaena haematina* kollar, 1849**	*Ferulago carduchorum* (Apiaceae)	Non-endemic	75	34
***Zygaena kermanensis* tremewan, 1975**	*Eryngium billadieri* (Apiaceae)	Endemic	77	335
***Zygaena loti* ([denis & schiffermüller], 1775)**	*Securigera varia* (L.) Lassen (Fabaceae)	Non-endemic	262	2921
***Zygaena manlia* lederer, 1870**	*Bupleurum exaltatum* (Apiaceae)	Endemic	22	422
***Zygaena mirzayansi* hofmann & keil, 2011**	*Eryngium billardieri* (Apiaceae)	Endemic	10	335
***Zygaena nocturna* ebert, 1974**	*Eryngium billardieri* (Apiaceae)	Endemic	35	335
***Zygaena pseudorubicundus* klir & naumann, 2002**	*Falcaria vulgaris* Bernh. (Apiaceae)	Endemic	33	1502
***Zygaena speciosa* reiss, 1937**	*Trachydium depressum* (Boiss.) Boiss.; *Semenovia tragioides* (Apiaceae)	Endemic	26	48; 24
***Zygaena tamara* christoph, 1889**	*Eryngium billardieri* (Apiaceae)	Non-endemic	123	335
***Zygaena turkmenica* reiss, 1933**	*Eryngium billardieri* (Apiaceae)	Non-endemic	108	335
***Zygaenoprocris duskei* (grum-grshimailo, 1902)**	*Atraphaxis spinosa* L. (Polygonaceae)	Endemic	47	307

To compare the current and future distribution of the species, we selected 19 bioclimatic variables (including different climatological variables for temperature and precipitation; see https://chelsa-climate.org) for the current and three future climate scenarios. We selected a subset of the variables avoiding any high multicollinearity using pairwise Pearson's correlation coefficients ($r > 0.75$). We also tested multicollinearity using *VIF* (Variance Inflation Factor) from the *usdm* package in R (Naimi et al. 2014; R Core Team 2022; see Supplementary Information I, Fig. S1). Furthermore, a PCA (Principal Component Analysis) was performed to explore the contribution of environmental variables to the principal components (*ade4* package; Dray & Dufour 2007; Fig. S1). Finally, we used five of the variables to calibrate our models; these variables mainly represent the extreme levels of temperature and precipitation (for more details, see https://chelsa-climate.org), as: 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).

Table 2: List of the future climate scenarios and short description of their features.

Scenario	**Name**	**CO_2 (ppm)**	**Temperature (°c)**
SPP126	green	400	+ 1
SPP370	Middle of the road	800	+ 3.9
SPP585	Fossil-fueled Development	1200	+ 4.7

Data preparation

Most of the analyses were run in the R environment (version 4.2.1; R Core Team 2022). Using the *raster* and *biomod2* packages, a Presence-Absence Matrix (PAM) for both Zygaenidae and their host plants were generated (Hijmans 2022; Thuiller et al. 2021). Depending on the number of occurrences, we generated 15 times pseudo-absences for each species within a 500 km buffer around the occurrences to consider the enough environmental space and generate informative pseudo-absences (Barbet-Massin et al. 2012). The PAM includes binary data for the presence/absence of the species (1 and 0, respectively) and extracted values from environmental variables for current and future climate scenarios. The PAMs were created for further analysis in the *ecospat* and *biomod2* packages (Broennimann et al. 2022; Thuiller et al. 2021). The *ecospat* package includes a set of comprehensive functions to study species distribution, and niche qualification and comparison (Di Cola et al. 2017).

Species distribution modeling

Tuning the models

The following setup was applied to tune the computing function in *biomod2. Modeling* (*biomod2*) and *ecospat.ESM.Modeling* (e*cospat*). The functions were run for 10 replicates each; 80% of the occurrences were put aside to test the model. Table 3 depicts the mean values for evaluation of the model performance for each species based on Kappa (also known as Cohen's kappa coefficient), TSS

(True Skills Statistic), and AUC (Area under the ROC Curve) metrics. To ensemble final models, we set a threshold for the models higher than AUC/ROC 0.7. Furthermore, models with higher values for TSS (> 0.7) were selected for projecting the species distribution to future climate scenarios (Table 3). Finally, we report the contribution of environmental variables and host plants for each species of zygaenid moth for both SDM and ESMs approaches (for more details see SI. section III).

Table 3. Results of model evaluation for the studied species. Here the average of each metric is represented. (H) and (M) stand for Host plant and Moth, respectively. The table is sorted alphabetically based on species names of moths and host plants.

Species	**KAPPA**	**TSS**	**AUC**	**Approach**
Rhagades brandti (M)	0.598	0.867	0.953	ESMs
Zygaena aisha (M)	0.846	0.973	0.993	ESMs
Zygaena araxis (M)	0.287	0.715	0.908	ESMs
Zygaena cuvieri (M)	0.598	0.778	0.954	SDM
Zygaena ecki (M)	0.920	0.989	0.996	ESMs
Zygaena fredi (M)	0.744	0.868	0.979	SDM
Zygaena ginnereissi (M)	0.650	0.935	0.957	ESMs
Zygaena haematina (M)	0.636	0.909	0.982	ESMs
Zygaena kermanensis (M)	0.515	0.888	0.964	ESMs
Zygaena loti (M)	0.407	0.673	0.905	SDM
Zygaena manlia (M)	0.559	0.833	0.941	ESMs
Zygaena mirzayansi (M)	0.699	0.929	0.975	ESMs
Zygaena nocturna (M)	0.798	0.9664	0.984	ESMs
Zygaena pseudorubicundus (M)	0.712	0.847	0.976	SDM
Zygaena speciosa (M)	0.8414	0.9403	0.982	ESMs
Zygaena tamara (M)	0.639	0.821	0.966	SDM
Zygaena turkmenica (M)	0.540	0.756	0.945	SDM
Zygaenoprocris duskei (M)	0.444	0.690	0.909	SDM
Prunus eburnea (H)	0.560	0.782	0.933	SDM
Atraphaxis spinosa (H)	0.358	0.597	0.862	SDM
Bupleurum exaltatum (H)	0.423	0.664	0.906	SDM
Eryngium billardieri (H)	0.431	0.702	0.922	SDM
Falcaria vulgaris (H)	0.311	0.580	0.868	SDM
Ferulago carduchorum (H)	0.446	0.849	0.960	ESMs
Onobrychis cornuta (H)	0.490	0.721	0.934	SDM
Securigera varia (H)	0.276	0.588	0.862	SDM
Semenovia tragioides (H)	0.477	0.758	0.902	ESMs
Trachydium depressum (H)	0.456	0.787	0.939	SDM

Modeling the species distribution

Most of the species in our dataset are endemic to the country with a very narrow distribution range. Therefore, the low number of occurrences were not enough to apply conventional species distribution modeling (SDM), since the limited number of occurrences in the SDM may result in model overfitting (Della Rocca et al. 2019; Di Cola et al. 2017). To avoid this, we used the Ensemble Small Models (ESMs) approach in the *ecospat* package (Broennimann et al. 2022). The results of previous works demonstrated that the ESMs could reduce overfitting of the models regarding species with few occurrences (e.g., Breiner et al. 2018; Della Rocca & Milanesi 2022; Herrera et al. 2022). We computed the SDMs for the species with more than 30 unduplicated records using the *biomod2* package (Thuiller et al. 2021; Table 1). We executed our SDM and ESMs using maximum entropy (MaxEnt) machine learning algorithms, as they have the best performance, particularly for presence-only data (Elith et al. 2011; Fourcade et al. 2014; Phillips & Miroslav 2008; Phillips et al. 2006). The model performance was evaluated using different metrics such as TSS (True Skills Statistic), AUC/ROC (Area under the Receiver Operating Characteristic Curve), and Boyce Index. The latter has been designed to evaluate the performance of the models regarding presence-only data in the *ecospat* package (Di Cola et al. 2017; Table 3).

Host plants as abiotic variable

To import the host plant distribution in our model as a predictor, we first modeled the distribution of each host plant as it was described for zygaenids above and then used the result as predictor in combination with other abiotic variables in our models for each climate scenario (Table 2). Depending on the number of occurrences and distribution pattern we used SDM or ESMs to model the species distribution of the host plants and projected it to the future climate scenarios (Table 3). In case of host plants with a high number of occurrences (*Securigera varia* Lassen and *Falcaria vulgaris*), the coordinate dataset was thinned by two steps using the *gridSample* function from the *dismo* package, which thinned the dataset by selecting one record per pixel. Then the result of *gridSample* was used for further thinning steps using function *thin* from *spThin* (Aiello-Lammens et al. 2015). The *thin* function randomly keeps the occurrences with a user defined distance from each other (we considered a distance of 20 km as suitable).

Finally, to standardize the interpretation of the modeling products, we rescaled the resulting raster files from MaxEnt for habitat suitability. Raster files of habitat suitability were rescaled using omission of 10% of the lowest probabilities at the species records of SDM and ESMs predictions. In the next step, using the *mess* function in the *dismo* package, multivariate environmental similarity surfaces (MESS) were computed to assess the occurrence of extrapolation areas when projecting the models outside of their training range (Elith et al. 2010). Then values of MESS were used to evaluate accuracy of resulting habitat suitability in the future scenarios (the full projections of the species distribution under each climate-scenario are shown in SI: Fig. S2 – S30). In this study, we used a reclassified version of MESS to highlight those regions where at least one of the predictors exceed the training range (Rödder et al. 2013). The positive values of MESS were assigned to 0 and negative values to 1. This modification effectively characterizes the similarity or dissimilarity between the surveyed pixels and all the areas under study.

Area of habitat suitability

The predicted layer of habitat suitability can depict a wide range of areas as suitable habitats for a given species, including areas which are unlikely to be accessible. Therefore, to delimit the real suitable habitat we cropped the predicted layers for the current and future climate scenarios with a buffer of 50 km for a hull polygon of species occurrence using the *rangemap* package (Cobos et al. 2021; Soberón and Peterson 2005). We considered the area with the higher probability (> 25% and > 50%) within the buffer, as the area where species might be present in each climate-scenario. The area of the raster pixel with presence of the species were calculated in km^2 (Table 4). Furthermore, we only accepted the areas after subtracting the overlap of negative values for MESS which indicate extrapolation (Table 4). Table 4 depicts the area of current species range and the percentage of remaining areas compared with current species range under each future climate scenarios for values of habitat suitability more than 25% and 50%.

Species range shift

The PAM of species was generated from the raster values with the high probability for each species (> 50%). This PAM was used to look at the species' altitudinal preference for current and future climate scenarios, and to explore the overlap between species and their host plant. The elevation values were extracted for each simulated species' occurrence from the digital model for the earth elevation (Global Digital Elevation Model, ver. 3; www.nasa.gov), then density graphs were generated with the *ggplot2* package. Finally, we used the *raster.overlap* function from the *ENMTools* package to measure the overlap between the habitat suitability of moths and host plants (Warren et al. 2008; Warren & Dinnage 2023). The *raster.overlap* has been developed to measure the niche overlap resulting from species distribution modeling and has several metric values to explore the niche overlap. We used two metrics to explore the overlap between moths and their host plant, Schoener's similarity (D) and similarity statistic (I), of which both will result in a value between 0 (no overlap), and 1 (identical niche prediction). While the former has been used because of its simplicity and long-term use in biological interpretation, the latter, which is a modification of the Hellinger distances, is a measure of the similarity between two probability distributions and was developed to compare the community composition of different sites (Rödder & Engler 2011; Warren et al. 2008). Additionally, we applied the Moran's I and Greay functions from the *spdep* package to check our data for any potential spatial autocorrelation (SAC; Bivand & Wong 2018; Dormann et al. 2007; see Supplementary Information II).

Table 4. The areas of current species range of zygaenid species and their host plants and the percentage of remaining areas under future climate scenarios (for higher probability values > 25% and > 50%). (H) and (M) stand for Host plant and Moth, respectively. The table is sorted alphabetically based on species names of moths and host plants.

Species	**Current (km^2)**		**Spp126 (%)**		**Spp370 (%)**		**Spp585 (%)**	
Habitat suitability	**> 25%**	**> 50%**	**> 25%**	**> 50%**	**> 25%**	**> 50%**	**> 25%**	**> 50%**
Rhagades brandti $^{(M)}$	102686.7	54678.6	67.8	48.1	38.4	13.8	27.6	4
Zygaena aisha $^{(M)}$	4639.7	2454.2	25.4	17.5	1.2	0	0.4	0
Zygaena araxis $^{(M)}$	186591.2	112970.6	81.5	80	43.8	40.9	36.5	34.1
Zygaena cuvieri $^{(M)}$	316258.9	186720.1	79	65.7	35.8	17.4	24.2	11.2
Zygaena ecki $^{(M)}$	13461.1	5761.1	84.3	80.9	49.7	31.3	38.4	16.5
Zygaena fredi $^{(M)}$	67194.8	42923.0	42.4	29.2	8.4	3.7	3.8	2
Zygaena ginnereissi $^{(M)}$	2474.3	1695.2	23.5	12	0.2	0	0.1	0
Zygaena haematina $^{(M)}$	57728.8	26399.5	72.1	48.8	49.2	14.6	24.8	3.5
Zygaena kermanensis $^{(M)}$	86523.2	49163.8	64.8	47.6	27.5	10.1	18.1	2.9
Zygaena loti $^{(M)}$	1006950.3	656162.5	147.7	152.2	96.9	100.2	69.7	73.5
Zygaena manlia $^{(M)}$	30836.7	13964.1	87.9	79.9	65	44.7	60	23.2
Zygaena mirzayansi $^{(M)}$	24751.1	14780.1	57.3	30	8.3	1.2	3.8	0
Zygaena nocturna $^{(M)}$	43598.3	26065.8	56.6	36.3	27.4	3.4	13.6	0.1
Zygaena pseudorubicundus $^{(M)}$	63919.7	37976.8	117.6	117	75.7	67.6	61.7	61.4
Zygaena speciosa $^{(M)}$	8822.5	2445.9	82.7	72.5	48	20.8	45.2	17.6
Zygaena tamara $^{(M)}$	141103.0	90574.7	83.2	85.2	36.2	34.4	30.4	27.6
Zygaena turkmenica $^{(M)}$	335157.7	208340.0	64.9	55.2	28.3	26.7	23	21.5
Zygaenoprocris duskei $^{(M)}$	330157.9	232228.2	73.7	57	46.6	28	35.4	18
Prunus eburnea $^{(H)}$	236505.8	118533.4	68.5	80.2	43	51.6	34.9	42.1
Atraphaxis spinosa $^{(H)}$	1524625.7	893966.3	68.1	80.2	44.5	51.6	35.7	42.1
Bupleurum exaltatum $^{(H)}$	1528864.5	825909.2	83.5	79.2	62.4	58.1	55.2	48.4
Eryngium billardieri $^{(H)}$	548955.2	281025.2	81.3	65.9	45.6	36.9	41.6	30.3
Falcaria vulgaris $^{(H)}$	5341688.0	3257048.1	111.4	114.4	113.1	10.8.5	108.8	110.2
Ferulago carduchorum $^{(H)}$	84657.7	32707.2	93.5	96.8	135.1	146.9	130.9	143.6
Onobrychis cornuta $^{(H)}$	607871.7	308346.5	65.7	45.8	39.9	27.1	33.5	21.1
Securigera varia $^{(H)}$	6390915.4	3832141.5	104.2	119.3	110	103.3	110.1	101.7
Semenovia tragioides $^{(H)}$	286773.9	109990.1	107.9	108.3	116.7	55.8	154.6	67.1
Trachydium depressum $^{(H)}$	278860.8	119916.2	71.4	63.7	49.4	38.1	46	28.7

Results

Overall, considering the most probable habitats of zygaenid species (> 50%), our results show that more than 80% of the studied species will lose around 30%, 70%, and 75% of their habitat suitability under future climate scenarios (Spp126, Spp370, and Spp585) compared to their current distribution, respectively (Table 4; Fig. 2). Although under future climate scenarios some of the non-endemic species of zygaenids and their host plants will experience an expansion in their current species range e.g., *Z. loti*, *F. vulgaris*, *S. varia*, most endemic species and their host plants will lose a dramatic area of their ranges (Table 4, Fig. 2).

Species richness and endemism

Results of the current study suggest that most of the Zygaenidae species in Iran are distributed across mountainous areas in the north and the western half of the country (Fig. 1). However, as evident in Fig. 1 richness of endemic species is more pronounced along the southern parts of Zagros Mountain, and mountainous regions of Kerman province in the south. Furthermore, central, and eastern parts of Alborz Mountain and the southern areas of Kopet-Dagh Mountain are other regions with a high number of endemic species. Ghohrud Mountain, a chain of segregated high-elevation mountains along the western margin of the Central Basin and parallel to the Zagros Mountain, is another hotspot of endemism (Fig. 1).

Habitat suitability under climate change

Results of this study demonstrate that most Zygaenidae species and their host plants will, at least to some extent, experience a shrinking in their current distribution range under both optimistic and pessimistic climate scenarios by the end of this century (Table 4; Fig. 2). The degree of habitat loss does show a significant correlation with endemism. There is a distinct difference between the response of endemic and non-endemic species to climate scenarios. As shown in Table 4 and Fig. 2, all non-endemic species will experience a significantly smaller reduction in their species range under each climate scenario. The only exception is *Z. haematina*, which is not endemic for Iran but mainly distributed from the southeast Turkey toward the center of Iran (endemic in Zagros Mountain). On the other, except for one of the endemic species (*Zygaena pseudorubicundus*), other endemic species show a dramatic decline in their ranges. Unlike other endemic species, the rate of habitat loss in *Z. pseudorubicundus* is not significant, and as shown in Table 4 and Figs. 2 and 3, the area of habitat suitability for the species is shrinking by 40% even under pessimistic (Spp585) climate scenarios.

However, the rate of habitat loss for the species in the eastern and southern part of its range (Zagros Mountain) is much higher than the northern distribution across the central Alborz Mountain Our model predicts that the Zagros's population of *Z. pseudorubicundus* might shrink significantly under pessimistic climate scenarios (Table 4, Fig. 3).

In most areas, habitat loss is much more severe under the pessimistic scenarios (Spp370 and Spp585; Table 4). The models predict the complete vanishing of habitat suitability for species like *Zygaena aisha*, 1980, *Z. mirzayansi*, and *Z. ginnereissi*, considering area with higher probability for species distribution (> 50%; Table 4; Figs. 2 & 4). Additionally, the suitable habitat area for species like *Z. nocturna, Z. fredi, Z. kermanensis*, *Z. haematina*, and *Rhagades brandti,* is getting dramatically smaller than the current species range (< 0.1 %, < 2%, < 2.9%, and 4%, respectively) under pessimistic scenarios (Spp585). However, the rate of habitat loss is lower for non-endemic species, like *Z. loti* (< 25%; Table

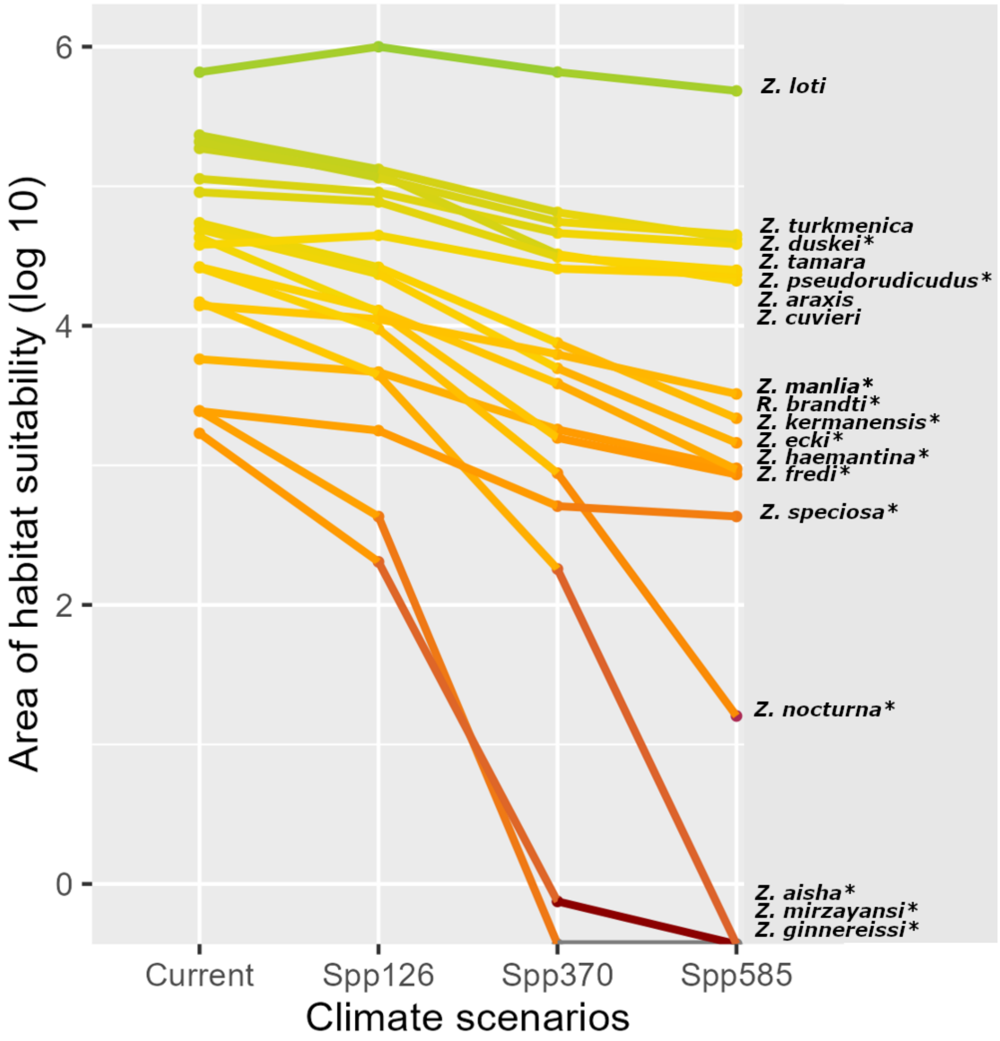

Figure 2. A comparison between the area of habitat suitability for the Zygaenidae species in current and future climate scenarios (Spp126, Spp370, Spp585). The gradient of color from green to dark red is comparable with the rate of habitat loss, which is significantly higher for endemic and narrow-distributed species compared with non-endemic species. (*) indicates the endemic species.

4; Fig. 2).

A bit less pronounced, we detected a similar trend of species-range shifts for the host plants (Table 4). As already discussed for the zygaenid moths, non-endemic species of host plants with wider distribution range will be affected less and even experience an expansion in their ranges e.g., *Securigera varia*, *Falcaria vulgaris*. However, the rate of habitat loss even in non-endemic species with narrower species range such as *Onobrychis cornuta*, *Eryngium billardieri* is higher (Table 4). The rate of habitat loss for the host plant species is much higher in southern parts of the country compared to its northern areas.

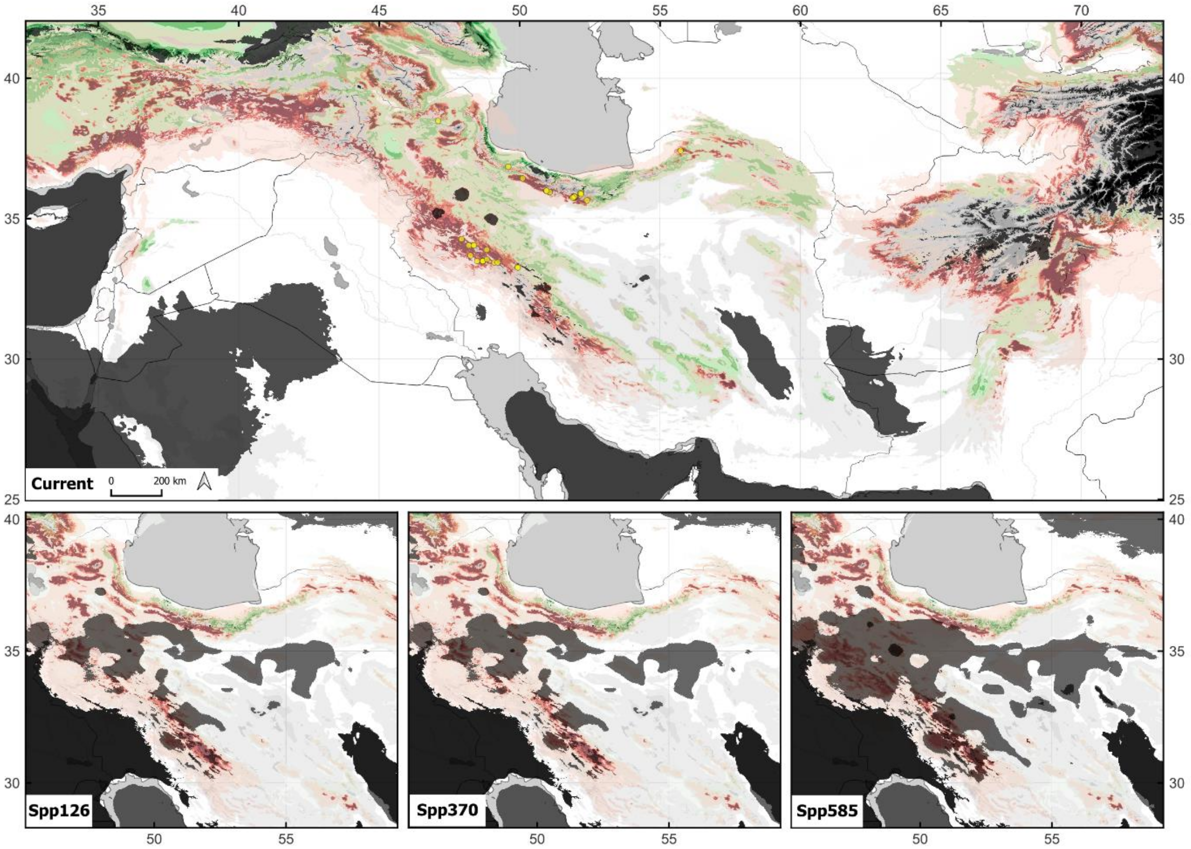

Figure 3. Forecast of endemic species, *Zygaena pseudorubicudus* and its host plant *Falcaria vulgaris* for current and under three climate scenarios (Spp126, Spp370, Spp585) by the end of the century in Iran. The yellow points represent occurrences of the species in our dataset; Gradient of red represents habitat suitability for the moth (*Z. pseudorubicudus*), and gradient of green represents habitat suitability for the host plant (*F. vulgaris*), the intensity of the color depicts the probability of species presence. Areas of potential extrapolations (MESS) are indicated as grey shading for both moth and host plant.

Our results suggest a higher impact of climate change, and particularly global warming, on the southern and central regions of the country. *Zygaenoprocris duskei*, a monophagous species, has a narrow distribution from the center to the southeast of Iran, and its larvae feed only on the *Atraphaxis spinosa* (Fig. 5). Under the pessimistic climate scenarios (Spp370, and Spp585), the host plant will lose most of its range in southern Iran and will shift towards higher latitudes, which will result in habitat loss and habitat fragmentation of *Z. duskei* (Fig. 5).

There are two general trends visible in our results: a) shifting in the ranges towards higher latitude for mainly non-endemic species, and b) shifting of species range towards higher elevation in the endemic species (Figs. 6, 7 & 8). *Zygaena loti,* which lives on the *Securigera varia* as its host plant (in Iran), is mainly distributed in the Alborz Mountain, the Caucasus, the Transcaucasus, Turkey, and southeastern Europe (Fig. 6). In response to the different climate scenarios, the area of habitat suitability of *Z. loti* will be stable (< 25% reduction under Spp585). Although the species will move towards higher latitudes in general, the population in Alborz Mountain will shift to higher elevations. The same distribution pattern can also be detected in distribution ranges of other non-endemic species like *Zygaena tamara*, and *Zygaena araxis*.

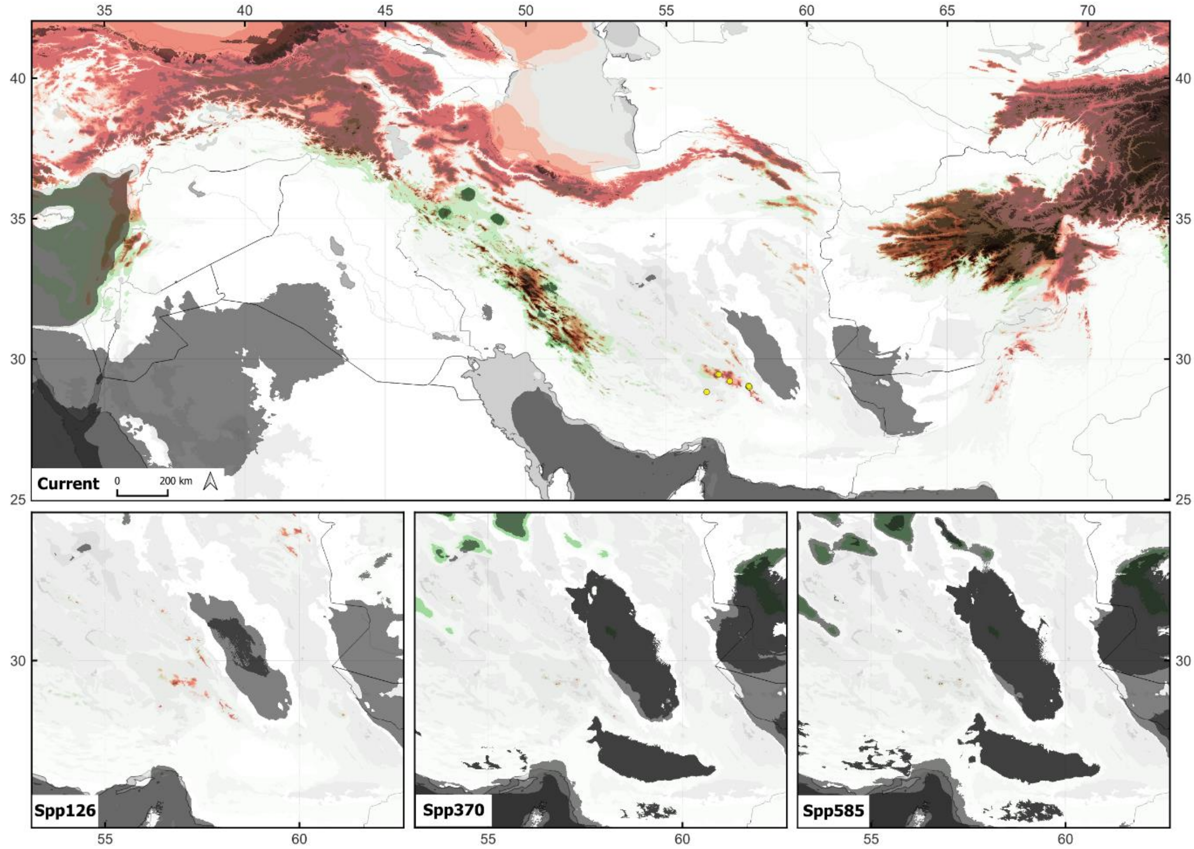

Figure 4. Forecast of endemic species, *Zygaena aisha* and its host plant *Ferulago carduchorum* for current and under three climate scenarios (Spp126, Spp370, Spp585) by the end of the century in Iran. The yellow points represent occurrences of the moth species in our dataset; Gradient of red represents habitat suitability for for the moth (*Z. aisha*), and gradient of green represents habitat suitability for the host plant (*F. carduchorum*), the intensity of the color the probability of species presence. Areas of potential extrapolations (MESS) are indicated as grey shading for both moth and host plant.

On the other hand, the species with narrower distribution range will experience a dramatic decline in their current range under all the future climate scenarios (Figs. 4, 5, 7, & 8). The endemic species, *Zygaena ecki*, is one of those species with a small distribution range in the central and eastern part of Alborz Mountain (Figs. 7 & 8d). Under pessimistic climate scenarios the species will lose most of its eastern distribution, particularly at the high elevation of Shahkuh Mt. in Semnan Province (> 84% reduction). A similar trend is observed for *Onobrychis cornuta*, the host plant of *Z. ecki*. (Fig. 7).

Moving toward higher elevation is more pronounced for endemic species e.g., in *Z. kermanensis*, and *Z. nocturna* (Figs. 8e & f), while species with wider distribution across central Asia to western Europe, do not show any significant altitudinal shifts in their species range, e.g., *Z. loti* (Fig. 8c). The results of the overlapping of habitat suitability show no significant gap in species range between zygaenid species and their host plResults of model evaluation revealed that precipitation amount of the wettest month (bio13) has highest contribution in modeling distribution for both zygaenid moths and their host plants (SI. Section III). On the other hand, while bio7 (annual range of air temperature) and distribution of host plants play an important role on prediction of species range of moths, daily minimum air temperature of the coldest month (bio6), has a greater influence on the species distribution of the host plants (SI. Section I).

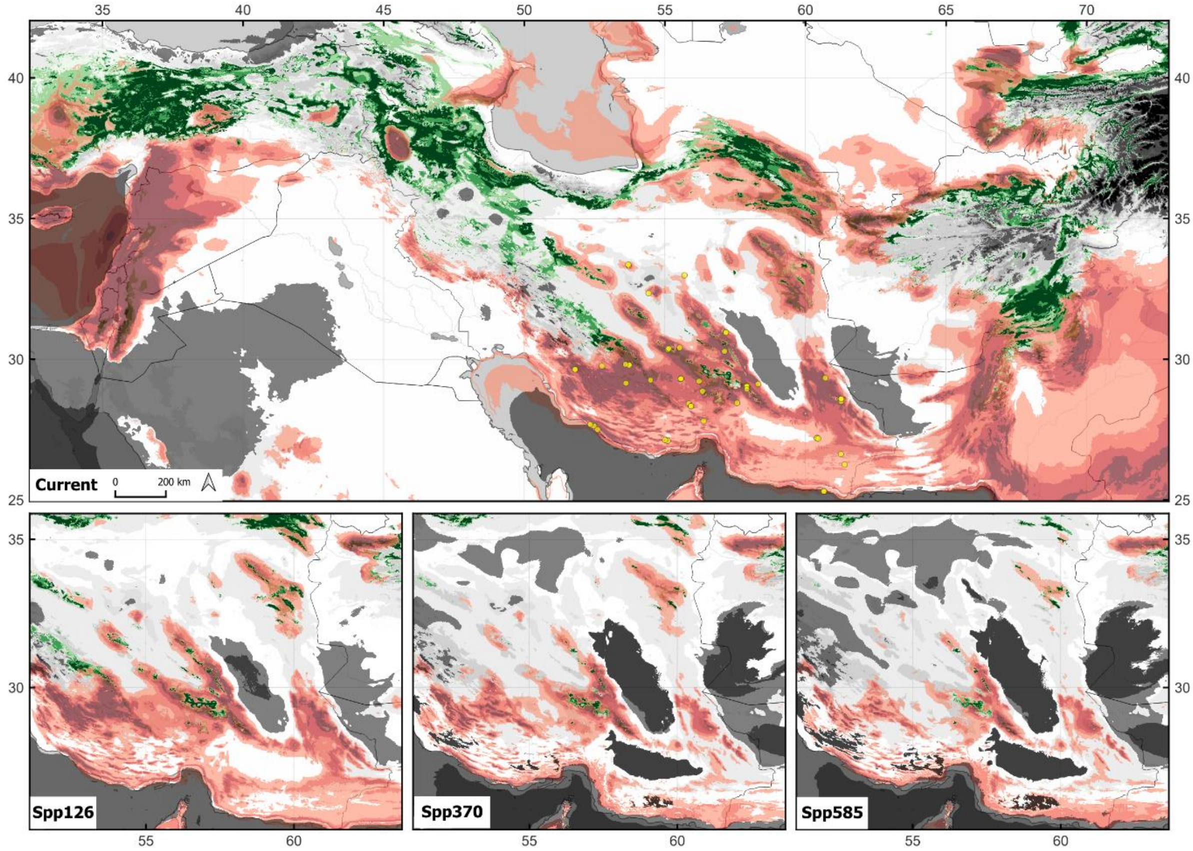

Figure 5. Forecast of endemic species, *Zygaenoprocris duskei* and its host plant *Atraphaxis spinosa* for current and under three climate scenarios (Spp126, Spp370, Spp585) by the end of the century in Iran. The yellow points represent occurrences of the moth species in our dataset; Gradient of red represents habitat suitability for the moth (*Z. duskei*), and gradient of green represents habitat suitability for the host plant (*A. spinosa*), the intensity of the color depicts the probability of species presence. Areas of potential extrapolations (MESS) are indicated as grey shading for both moth and host plant.

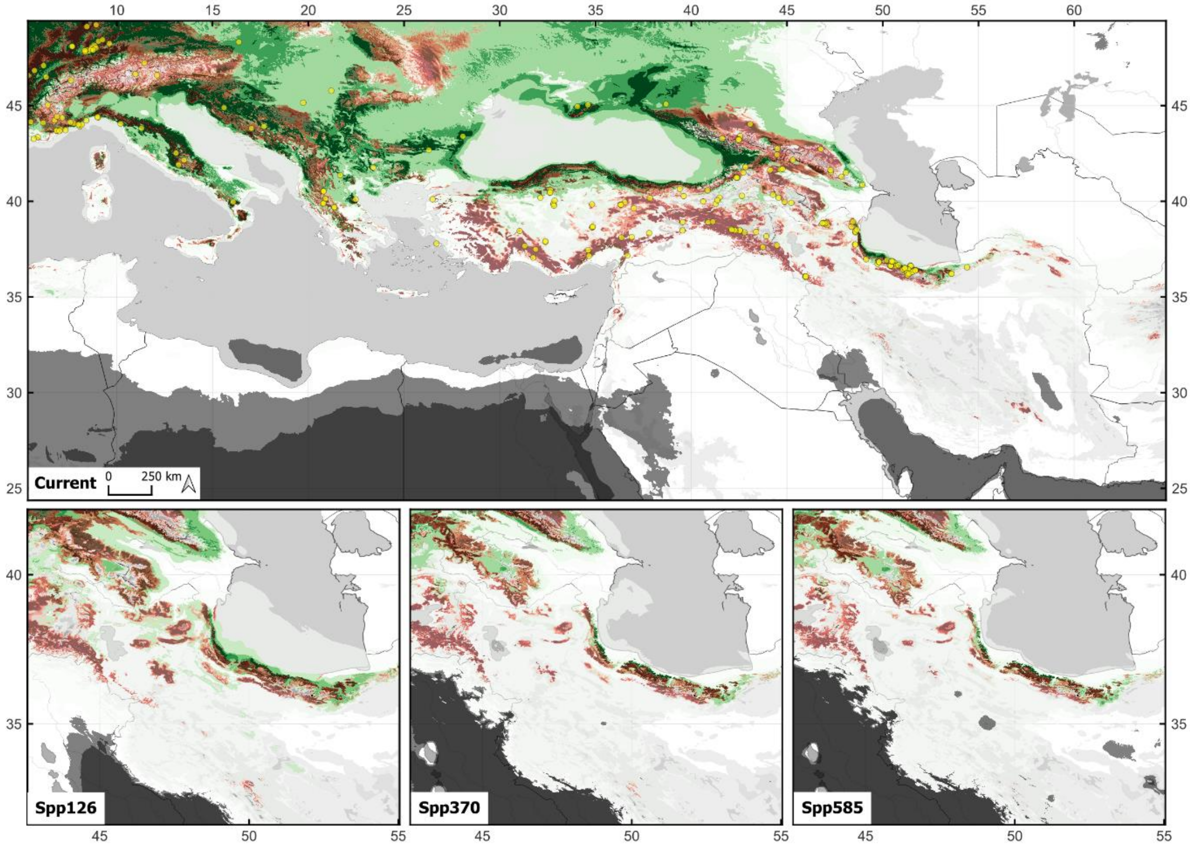

Figure 6. Forecast of non-endemic species, *Zygaena loti* and its host plant *Securigera varia* for current and under three climate scenarios (Spp126, Spp370, Spp585) by the end of the century in Iran. The yellow points represent occurrences of the moth species in our dataset; Gradient of red represents habitat suitability the moth (*Z. loti*), and gradient of green represents habitat suitability for the host plant (*S. varia*), the intensity of the color depicts the probability of species presence. Areas of potential extrapolations (MESS) are indicated as grey shading for both moth and host plant.

Discussion

Shifting towards higher elevation has been documented as a common response of different insect taxa and their host plants to climate change word wide (Biella et al. 2017; Della Rocca & Milanesi 2022; Filazzola et al. 2020; Rödder et al. 2021; Pyke et al. 2016). For instance, Rödder et al. (2021) revealed a constant altitudinal shift of species range for several butterflies in the eastern Alps during the past six decades. According to the results of the present study, zygaenid species of Iran will generally experience altitudinal range shift and a high habitat loss (> 64%) under the most extreme climate scenarios. However, the rate of habitat loss is twice as high for endemic species compared with non-endemics (Table 4; Fig. 2). This might be explained by the fact that non-endemic species with their wider distribution have access to a wider range of habitats and host plants compared to the endemics (Biella et al. 2017; Filazzola et al. 2020; Rödder et al. 2021; Pyke et al. 2016). As example, *Zygaena aisha* and *Z. ginnereissi* have an extremely restricted distribution range across the higher mountains of Kerman in the southern part of the Iranian central basin (Fig. 4). This region includes some mountains with elevation higher than 4000 m surrounded by the central deserts. Furthermore, zygaenids are not strong and fast fliers and therefore are highly dependent on their habitat (Naumann et al. 1999). Therefore, the response of these species to climate change will be limited to a shift toward higher elevation (Biella et al. 2017; Della Rocca & Milanesi 2022; Filazzola et al. 2020; Rödder et al. 2021; Fig. 4). On the other hand, non-endemic species like *Zygaena loti*, have more opportunities to move toward the higher latitudes across the Caucasus and Transcaucasia regions under extreme climate scenarios (Filazzola et al. 2020; Rödder et al. 2021; Table 4; Fig. 5).

High species-richness across mountains ranges

Our analyses depict a strong association between species richness and endemism with high-elevation regions across the main mountain ranges in most parts of the country: Zagros Mountain and Ghohrud Mountain, Alborz Mountain, Kopet-Dagh Mountain, Kerman-Yazd Masif and Makran-Taftan Mountain, which highlights the effect of the complex topography on distribution pattern of the Zygaenidae species. These results are in line with the previous results of the independent studies, which highlight the important roles of the mountainous areas to shape the biodiversity in Iran (Ghaedi et al. 2021; Noori et al. 2021; Noroozi et al. 2018, 2019; Yusefi et al. 2019). The above mentioned mountainous

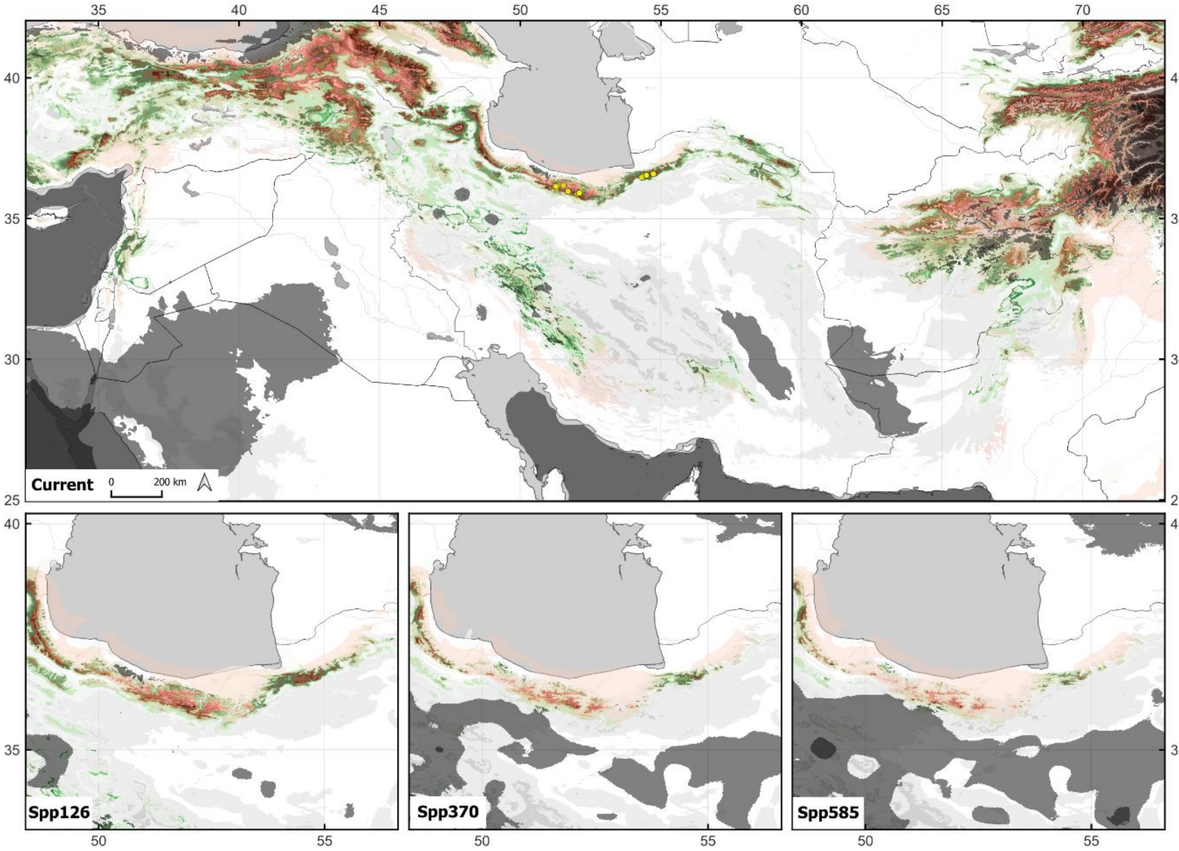

Figure 7. Forecast of endemic species, *Zygaena ecki* and its host plant *Ononbrychis cornuta* for current and under three climate scenarios (Spp126, Spp370, Spp585) by the end of the century in Iran. The yellow points represent occurrences of the moth species in our dataset; Gradient of red represents habitat suitability for the moth (*Z. ecki*) and gradient of green represents habitat suitability for the host plant (*O. cornuta*), the intensity of the color depicts the probability of species presence. Areas of potential extrapolations (MESS) are indicated as grey shading for both moth and host plant.

ranges increase the rate of isolation and at the same time provide a wide variety of microhabitats, which can act as refugia to buffer the effect of climate change for different species (e.g., Albrich et al. 2020; Della Rocca & Milanesi 2022; Djamali et al. 2012; Paknia & Rajaei 2015; Rajaei et al. 2013). Several studies suggested the dual effects of mountain ranges in Iran as corridors and simultaneously as a barrier to the speciation of different taxa (e.g., Ghaedi et al. 2021; Sanmartín 2003). The unique species composition of Zygaenidae in Iran, where many closely related species occur, suggests that Iran has played a significant role in the diversification of this family of moths (Hofmann & Tremewan 2017). Considering that most of above listed mountains fall in the Irano-Anatolian biodiversity hotspot, identifying species-diverse regions within this hotspot will help to delineating the areas with higher priority for conservation (Cañadas et al. 2014; Noroozi et al. 2018).

Heterogenous impact of climate change

Although climate change has impact on biodiversity at all levels, the risk of extinction is much higher for the species that occur in smaller and patchier habitats (Della Rocca & Milanesi 2022; Filazzola et al. 2020; Pardini et al. 2017; Rödder et al. 2021). Therefore, access of the species to larger and more diverse habitats may increase the ability of that species to tolerate climate change better (Filazzola et al. 2020; Franzén & Ranius 2004; Rödder et al. 2021). It has been well documented that species with more restricted ranges will suffer much more than species with a broad ecological amplitude from the rapid climate change (Bonelli et al. 2021; Rödder et al. 2021). Furthermore, species which are highly dependent on their host plants might experience a dual impact of climate change. Directly by effecting the species habitat suitability and indirectly by changing the interaction of species and host plants (Bellard et al. 2012; Blois et al. 2013; Filazzola et al. 2020).

In line with the previous studies, our results reveal a higher impact of climate change on the biodiversity in the center and south of the country than northern regions, which are the regions with higher species richness and pronounced endemism across mountainous areas (Fig. 1 & 5; Ashrafzadeh et al. 2019; Shamsabad et al. 2018). Different studies suggested a higher impact of climate change in the Middle East and especially in Iran, because of the high level of contribution to the emission of greenhouse gas (Daneshvar et al. 2019; Segan et al. 2016; Waha et al. 2017). As a general trend, our model predictions show that the impact of climate change even across a mountain range (e.g., Alborz Mountain) is not homogeneous. The eastern parts of the Alborz Mountain will be affected more than its western parts, which can be seen e.g., for *Zygaena ecki* (Fig. 7). This might be interpreted by heterogenous topology of the mountainous areas which provide a wide range of habitats with different climatic setups (Albrich et al. 2020; Djamali et al. 2012). Most of the endemic Zygaenidae species are distributed in the small zones above the tree line of mountains (Hofmann & Tremewan 2017; Keil, 2014). To this end, different studies confirmed the important role of mountain ranges in the configuration of the country's biodiversity (Noori et al. 2021; Noroozi et al. 2018; Yousefi et al. 2023, 2019).

Threats of Iranian Zygaenidae

Several studies have highlighted a significant gap between the current protected areas of the country and the most diverse regions for different groups of animals and plants, particularly in mountainous areas (Noori et al. 2021; Noroozi et al. 2023, 2019; Yusefi et al. 2019). The network of protected areas of the country is under intense pressure by human activities (Karimi & Jones 2020). For instance, overgrazing has been reported as one of the most important threats to natural habitats and particularly

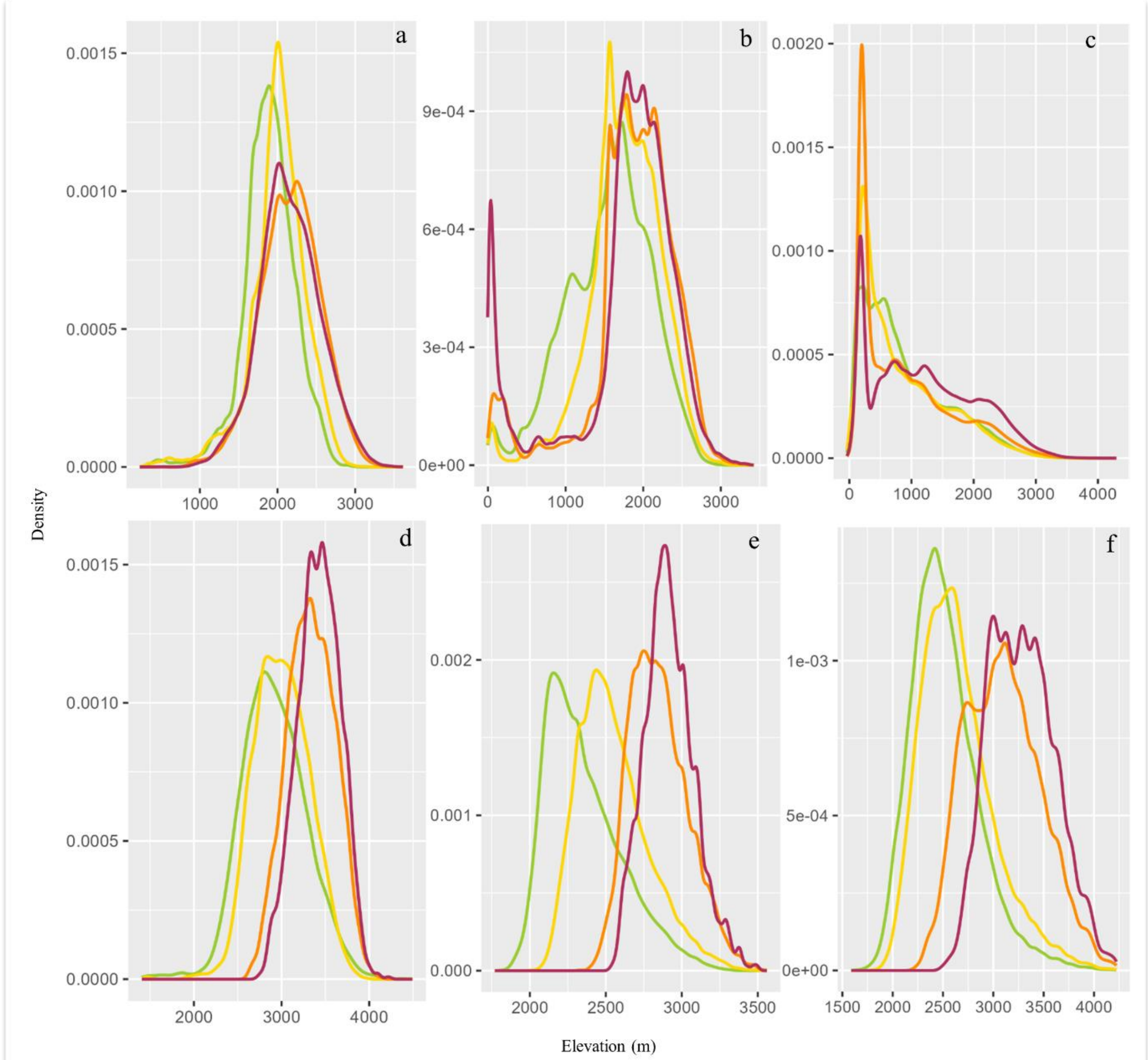

Figure 8. Elevational shifts in the species range of the Zygaenidae species for areas with higher habitat suitability (>50%) for: a) *Z. pseudorubicundus**; b) *Z. duskei**; c) *Z. loti*; d) *Z. ecki**; e) *Z. kermanensis*; f) *Z. nocturna**. Current = green, Spp126 = yellow, Spp360 = orange, and Spp585 = dark red. (*) indicates the endemic species.

high-elevation biodiversity in Iran (Karimi & Jones 2020; Jowkar et al. 2016). This factor has been suggested as one of the important factors which affect the habitat quality of the burnet moths (Franzén & Ranius 2004; Naumann et al. 1999).

Franzén & Ranius (2004) suggested that the high correlation between distribution of burnet moths and butterflies, reflecting the fact they have similar habitat requirements. Therefore, simulation of the future distribution pattern of the species can help to understand the effect of climate change not only on zygaenid moths, but also other groups of Lepidoptera and maybe other insects (Bellard et al. 2012). Consequently, defining higher priority areas for the conservation of vulnerable groups like Zygaenidae under ongoing climate change is inevitable. This will help scientists and decision-makers to estimate the extinction risk of the different species by investing limited resources for highly protecting species-diverse areas efficiently and develop target habitat management plans for habitats that are particularly at risk.

Limitation of the model and potential enhancements

While the insights gained from this study are valuable, it is important to acknowledge the inherent limitations in our approach. As previously discussed, most of the endemic zygaenid moths are in small populations that are highly localized, rendering it impractical to gather a more extensive dataset (Hofmann & Tremewan 2017; Keil, 2014; Naumann et al. 1999). This may increase the risk of model overfitting and the impact of spatial autocorrelation (SAC) on our analysis (Dormann et al. 2007). Our examination of SAC within the data reveals the chance for SAC for some of the species, particularly endemic once. Consequently, the results necessitate cautious consideration. To enhance the reliability of our findings, it is imperative to conduct more intensive surveys in the study area, thereby reducing the bias in sampling effort. Furthermore, incorporating other variables (i.e., land cover, topology, etc.) linked to the physiology and phenology of the zygaenid moths and their host plants could bolster the robustness of our results.

Conclusion

Rapid anthropogenic climate change impact on the current biodiversity and accelerates the risk of extinction higher than at any time on the planet earth (Pimm et al. 2014; Settele et al. 2016; Shivanna 2020). Climate change is not only affecting the habitat suitability of the species but also the interactions between species (Bellard et al. 2012; Blois et al. 2013). Estimating the reaction of different species to climate change may help to design more effective conservation strategies. Although the present study was limited to the species of the family Zygaenidae, it provides an example of how climate change will affect biodiversity unevenly at the level of a country. Our results show different responses of the endemic and non-endemic species to future scenarios of climate change. While non-endemic zygaenid species might move poleward, the endemic species may move towards higher elevations, especially due to their high dependence on their host plants/habitats and low flying ability. Our models predicted that higher mountains in the southern and central parts of Iran may be affected more severely than higher latitudes. Considering that the mountainous areas with high biodiversity are under high pressure from human activities due to being close the populated cities, expansion of the current network of protected areas toward regions with higher species diversity is an inevitable solution. However, designing an effective conservation practice depends on improving our understanding regarding the distribution pattern of different species, particularly the mega-diverse group of insects.

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▪ List of appendixes and supplementary information

The appendices and supplementary information for each study within this dissertation have been stored in a GitHub repository, available at:https://github.com/Asohasmik/Dissertation

Chapter II.

Appendix: The full list of elusive localities of Iranian Lepidoptera records. https://github.com/Asohasmik/Dissertation/tree/ceffcd37a795d30133a5425dbd87fdc14b28c77e/Chapter%20II

Chapter IV

Appendix I: A list for regularization and defining parameters of MexEnt for each species.

Suplementary Information I: Description of environmental variable selection for species distribution models, and full results of bioregionalization and modeling elevational distribution for selected families of Lepidoptera (Geometridae, Lycaenidae, and Zygaenidae). https://github.com/Asohasmik/Dissertation/tree/ceffcd37a795d30133a5425dbd87fdc14b28c77e/Chapter%20IV

Chapter V

Suplementary Information II:

Appendix I: A list for regularization and defining parameters of MexEnt for each species.

Appendix II: A full list for coverage and species richness of each protected area in Iran.

Suplementary Information II: Description of environmental variable selection for species distribution models, and additional results for potential conservation of each protected area in Iran. Statistical differences of coverage for each IUCN category for areas with higher conservation priority.

https://github.com/Asohasmik/Dissertation/tree/ceffcd37a795d30133a5425dbd87fdc14b28c77e/Chapter%20V

Chapter VI

Appendix I: The results of environmental variable contribution in the species distribution models. The appendix also provides the results for the Moran's I and Geary test to check for potential spatial autocorrelation.

Suplementary Information I: Description of environmental variable selection for species distribution models, and the results of habitat suitability for all the studied species at present and under three different climate scenarios in the future.

Suplementary Information II: The occurrence dataset was used in this study.

https://github.com/Asohasmik/Dissertation/tree/ceffcd37a795d30133a5425dbd87fdc14b28c77e/Chapter%20VI

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Eidesstattliche Versicherung

Declaration on oath

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare upon oath that I have written the present dissertation independently and have not used further resources and aids than those stated in the dissertation.

Stuttgart/ 13.05.2018

Ort/Datum

Unterschrift