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Review

Patterns of Zoological Diversity in Iran—A Review

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Abstract: Iran is a country characterized by high biodiversity and complex biogeographic patterns. Its diverse landscape and steep climatic gradients have resulted in significant faunal diversity and high level of endemism. To better understand these patterns, we investigated the historical environmental drivers that have shaped Iran's current geological and climatological conditions, and, consequently, have shaped the current zoological distribution patterns. Furthermore, we provide an overview of the country's zoological diversity and zoogeography by reviewing published studies on its fauna. We analyzed nearly all available catalogs, updated checklists, and relevant publications, and synthesized them to present a comprehensive overview of Iran's biodiversity. Our review reports approximately 37,500 animal species for Iran. We also demonstrated that the country serves as a biogeographic transition zone among three zoogeographical realms: the Palearctic, Oriental, and Saharo-Arabian, where distinct faunal elements intersect. This biogeographic complexity has made it challenging to delineate clear zoogeographical zones, leading to varying classifications depending on the taxon. The uplift of mountain ranges, in particular, has played a crucial role in shaping faunal diversity by serving as barriers, corridors, and glacial refugia. These mountains are largely the result of orogeny and plate collisions during the Mesozoic and Cenozoic eras, coupled with the development of the Tethyan Sea and the uplift of several ranges during the Miocene. Despite these insights, our understanding of biodiversity distribution in Iran remains incomplete, even for some well-studied taxa, such as certain vertebrate families and arthropods. We highlight the existing gaps in knowledge regarding zoogeographical patterns and propose approaches to address these gaps, particularly concerning less-studied species and the highly diverse group of insects.

Keywords: biodiversity hotspots; biogeography; climate oscillations; Iranian fauna; mountain uplift; macro-transitional zone

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1. Introduction

Iran is a large country in western Asia, its territory overlapping with two global biodiversity hotspots, the Caucasus and the Irano-Anatolian (Figure 1a,b) [1,2]. Despite its importance for global biodiversity as a 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 [3,4] (Figure 1a). But more importantly, an extensive review of the scattered literature on the topic is missing. Here, we aim to provide a comprehensive review of the geological and climatic setup, the animal diversity, and zoogeographical patterns to reveal larger-scale biodiversity and biogeographic paradigms. To achieve this aim, we subdivided this paper into four sections: first, we summarize the key abiotic drivers forming the current biodiversity, both at present and through past geographical periods; then, we review the current knowledge of the known Iranian fauna. Furthermore, we discuss the current distribution patterns of the Iranian fauna based on zoogeographical and phylogeographical studies. Finally, we list the gaps in knowledge regarding biodiversity in Iran and provide practical suggestions to tackle these gaps.

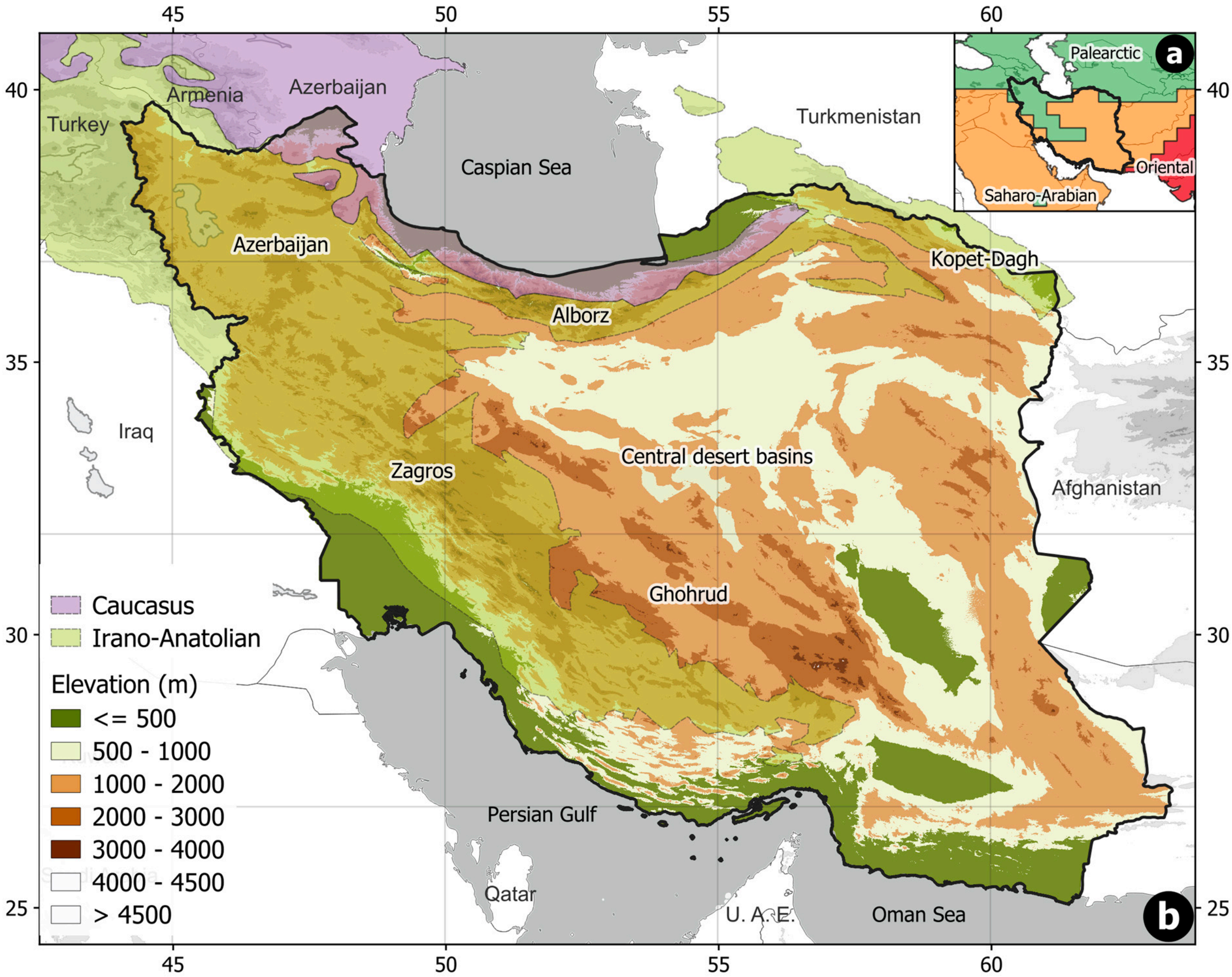

Figure 1. (**a**) Iran intersects with three global zoogeographical realms: Palearctic, Saharo-Arabian, and Oriental (adopted from [3]). (**b**) The western and norther regions of Iran belong to two of the global biodiversity hotspots (Caucasus and Irano-Anatolian).

2. Key Drivers of Current Biodiversity

2.1. 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 the 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 (Figure 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 [5–7], which gave rise to a mosaic of higher and lower mountain ranges in various shapes and degrees of erosion [5,8]. The two largest and highest mountain ranges are the Alborz and Zagros; the Alborz (or Elburz) Mountains extend along the northern 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 the southeast. The vast region located between these mountain ranges is known as the Central Iran basins, which is not a flat plain, but a region with high physiographic complexity containing several scattered large mountains and many small mountains in the central and eastern region of the country. The average elevation in the country is 900 m, ranging from −28 m at the seashores of the Caspian Sea to 5610 m at the Damavand peak, overall declining towards the coastal regions of the Persian Gulf and the Oman Sea (Figure 2) [5,9].

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 ranging from −6 to 21 °C in the coldest months and from 19 to 39 °C in the warmest months (Figure 2a) [9,10]. Likewise, the annual rainfall is highly variable, ranging from less than 100 mm in some parts of the Central Iran basins up to above 2000 mm in some parts of the Caspian Sea coasts (Figure 2b; Iran Meteorological Organization, http://www.irimo.ir/eng; Figure 2). Overall, 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) [9,11]. Precipitation variability is largely associated with the mountains, mainly the Alborz and Zagros mountain ranges (Mountains) in the north and west (Figure 1b) [12], which receive higher rainfall compared with lowlands. According to [13], Iran contains three (Mediterranean, Temperate, and Tropical) out of five world macro-bioclimates [14], including 11 of the 17 bioclimates that exist in these three macro-bioclimates. More recently, Yusefi et al. [15] identified eight climatic regions inside the country by using a model-based cluster analysis of 13 bioclimatic variables, mostly representing temperature and precipitation. The above-mentioned high geological and climatic heterogeneity results in high habitat diversity: seven of the fourteen described global biome types, including 19 different ecoregions, are found in Iran [16], which in turn gives rise to a substantial faunal and floral diversity.

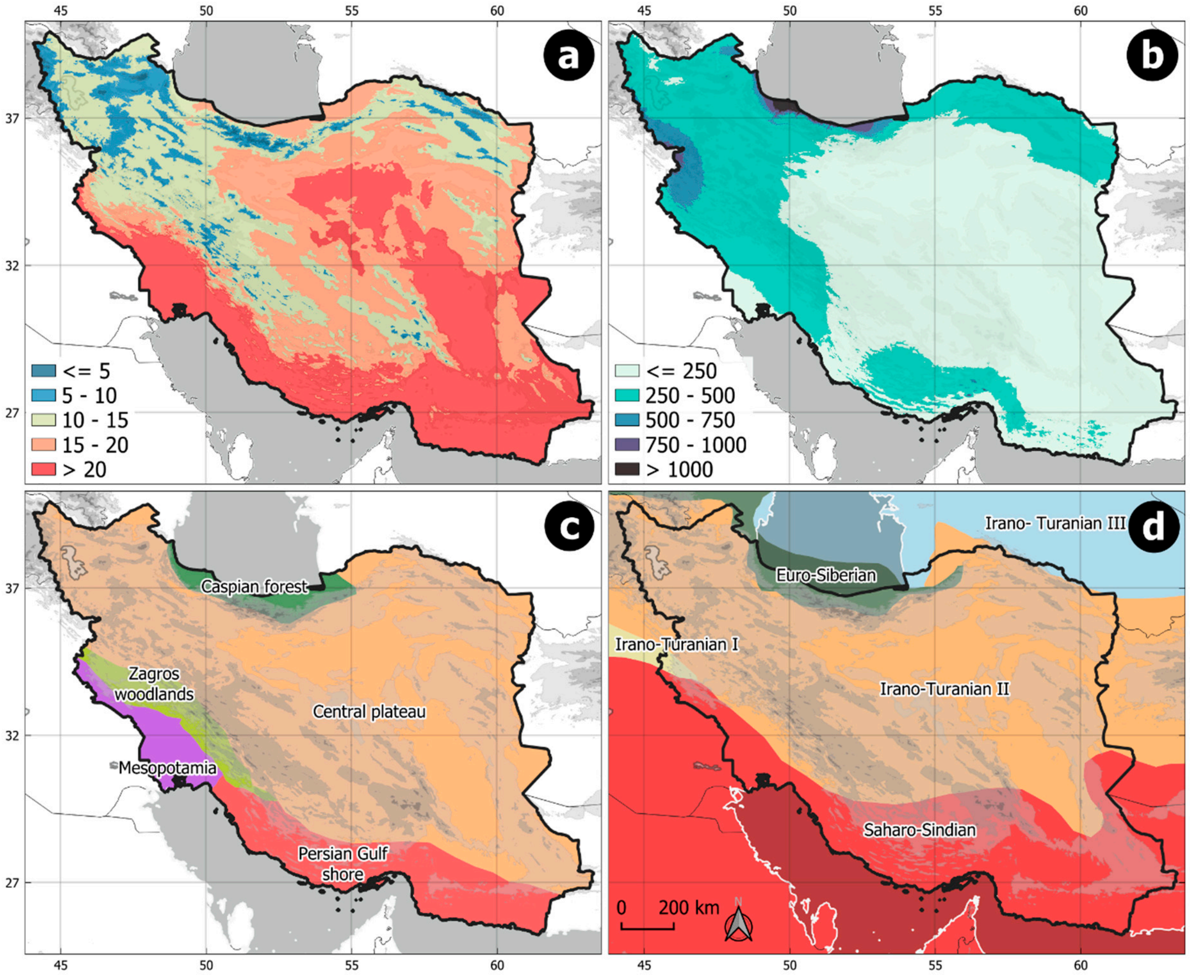

Figure 2. Maps of abiotic variables and historical regionalization for animals and plants of Iran. Maps for annual average (**a**) temperature (°C) and (**b**) precipitation (mm) in Iran between 1970 and 2000 (www.worldclim.org); (**c**) zoogeographic subdivisions of the country based on mammal data (adopted from Blanford 1876); (**d**) phytogeographic regions (adopted from White and Léonard 1991).

2.2. Geography, Geology and Climate—The Past

The current biodiversity of the country is not only dependent on the current conditions but is largely shaped by past geological events and climatic fluctuations. The collision of the Arabian and Indian Plates with Eurasia resulted in the uplift of several mountain chains in the north, west, and south of Iran [8]. Based on the literature, four major time periods played a large role in the current setup of the country's faunal diversity starting 4600 million years ago (MYA).

Gondwanaland–Laurasia collision: 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; Figure 3a), concurrent with the closure of the Paleo-Tethys Sea (Paleozoic) and opening the Neo-Tethys Sea in its wake [8,17,18]. Later, at the border of the late Triassic to early Jurassic (210–195 MYA), folding and uplifts occurred on the Central Iranian plate through the Cimmerian orogeny that resulted in the partial emergence of the Central Iranian plains from the sea [5,8]. 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 [19]. 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 Mountains [20] (Figure 3b).

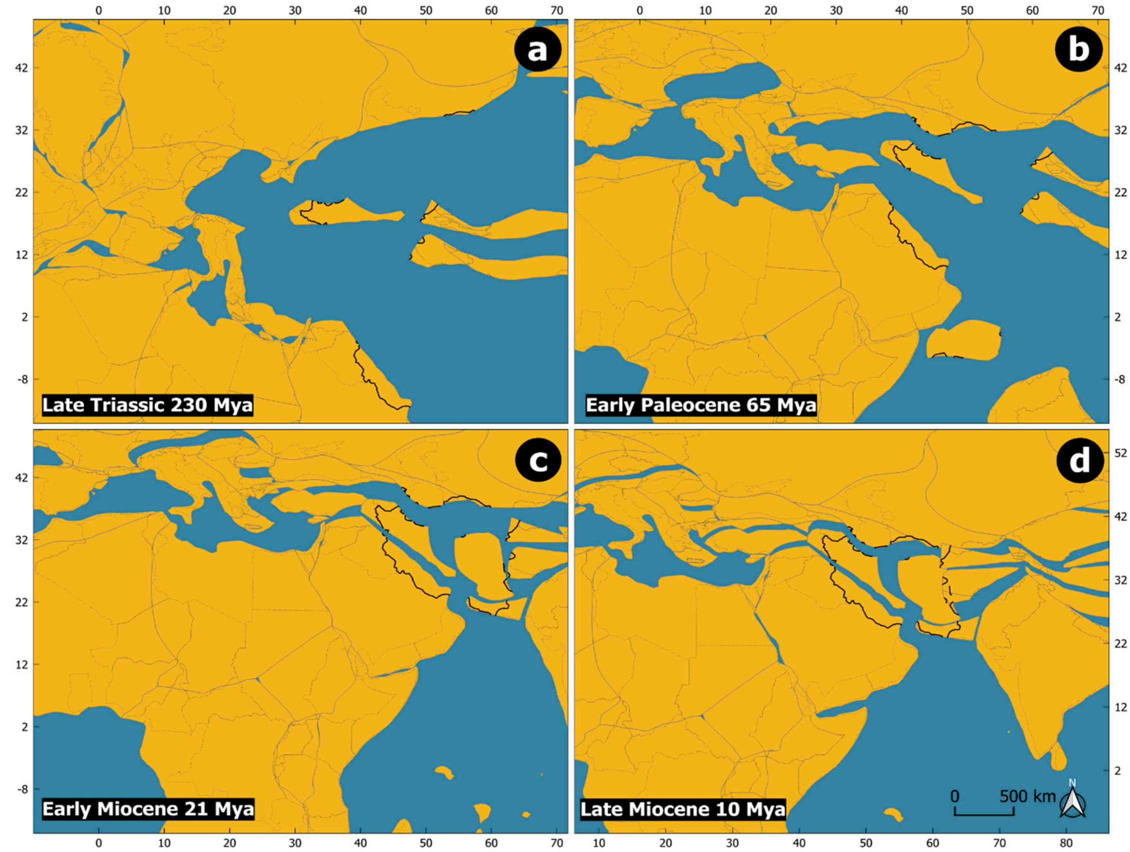

Figure 3. Position of microplates in Iran through time. (**a**) Cimmerian superterrane (microplates of Iran and neighboring countries) separated from northern regions of the Gondwana supercontinent and collided to the southern part of Laurasia. (**b**) The Tethyan seaway connected the major oceans. (**c**) Creation of *Gomphotherium* land bridge by the collision of the Arabian and Eurasian plates. (**d**) Closure of Tethyan seaway and uplifting of mountain ranges (Zagros and Alborz) in Iran.

Arabia–Eurasia collision: The Miocene period (on average 19 MYA; Figure 3c) mainly shaped Iran through the collision of the Arabian and Eurasian plates [21–23]. The Arabia–Eurasia collision created a wide zone of land deformation on the southern margin of Eurasia [22,23] that was concurrent with the retreat of the Qom Sea from eastern Zagros in central Iran and the Tethys Sea from the western Zagros Mountains. The Arabia–Eurasia collision created the first land bridge between Africa and Eurasia [24]. This land bridge, known as the *Gomphotherium* land bridge, made the first faunal exchange between Eurasia and Africa possible [19] (Figure 3c) and facilitated the range expansion and diversification of numerous taxa across Africa and Eurasia [25–29].

Uplifting of mountain ranges: The Arabia–Eurasia collision continued with a further uplift of the Zagros and the Alborz [8,30,31] (Figure 3d). Central Iran rose from the Qom Sea, and a wide zone of land deformation appeared on the southern margin of Eurasia [22], which formed new habitats and drove the isolation and speciation processes of various taxa [29,32–34]. During the uplift of the Zagros Mountains, savannah-like habitats in northwestern Iran disappeared and were replaced by mountainous landscapes [35,36].

Quaternary glacial and climate oscillations: The Pliocene was followed by a period of global climate oscillations and severe climatic changes in the northern hemisphere, including Iran (especially in northern and western parts of the country) [37–39]. The Middle East in general and Iran in particular [40–42] likely represented an important refuge area for many species of otherwise more northern latitudes (now Europe) [37,38]. 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 [43,44]. The Quaternary period affected the dynamics of the Zagros oak woodlands [45–47], which consequently influenced distribution patterns of linked faunal elements, especially insects [48,49]. 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; see, e.g., [34,40,50,51]. The last glaciation also changed the patterns of species distribution through the dropping of the sea levels, which, for instance, caused the Persian Gulf to dry up and turned it into a land bridge between the Iranian Plateau and the Arabian Peninsula, facilitating faunal exchange between these two land masses [52]. Rising sea levels after the glaciation, when the climate warmed, had a profound impact on the patterns of inter- and intraspecific variation among species (e.g., the Brandt hedgehog) [53].

3. Fauna: Biodiversity in Numbers

The steep climatic gradients and pronounced landscape heterogeneity have resulted in regions of exceptionally high biodiversity in western Asia, specifically Iran [54–59]. This relates not only to species richness but also to the high rates of endemism in the country [59–62]. There are more than 1327 species of vertebrates with 13% endemism (nationally). This includes 559 birds [63,64], 309 species of freshwater fishes [61,65], 241 reptiles, 22 amphibians [66–68], and 196 mammals [15,55,69]. Despite the known high biodiversity, the real number of animal species, even in the better-studied taxa like vertebrates, is believed to be underestimated [15]. This is even more severe for invertebrates.

The invertebrate fauna of the country is largely unexplored, and the number of species and rates of endemism remain unclear for many groups [57]. Despite this, a few taxa have been better studied, e.g., arachnids [70], collembolans [71], crustaceans [72], odonates [73], orthopterans [74], and lepidopterans [57]. Some invertebrate groups have been investigated at different taxonomic levels in taxonomic monographs or small checklists in recent years, e.g., [57,75–80]. However, knowledge about the total diversity of animal species is far from complete.

In this review, we conducted an extensive literature survey of the most recent monographs, checklists, and taxonomic revisions (Table 1; a full list of reviewed references and results is provided in the Supplementary Information S1 and S2 (SI S1 and S2)). Our survey revealed a total of some 37,500 known species, including 1327 species of vertebrates [58] (Figure 4; Table 1). In addition to the freshwater fishes, 763 species of fish were reported from the Persian Gulf, the Oman Sea, and the southern seashores of the Caspian Sea [81,82]. Our database also revealed some 32,600 known species of arthropods, including at least 27,093 known species of hexapods, 4560 chelicerates, 807 crustaceans, and 95 myriapods; see, e.g., [57,70,72,83–85] (Figure 4; Table 1). Besides arthropods, other species-rich phyla of invertebrates are nematodes with at least 1250 known species [86], followed by mollusks (ca. 600 species) [87]; rotifers (ca. 400 species) [88]; annelids (ca. 155 species) [89]; cnidarians (ca. 154 species) [90]; and echinoderms (ca. 124 species) [91,92] (Table 1).

Table 1. Number of known species for different animal taxa in Iran. N: Number of species.

Phylum	Subphylum	Class	Subclass	Order	N
Ctenophora					1
Porifera					11
Placozoa					1
Cnidaria					154
Myxozoa					10
Cephalochordata					3
Tunicata					7

Table 1. *Cont.*

Phylum	Subphylum	Class	Subclass	Order	N
Craniata		Agnatha, Chondrichthyes, Osteichthyes			1072
		Amphibia			22
		Reptilia			241
		Aves			559
		Mammalia			196
Echinodermata					124
Chaetognatha					19
Nematoda					1254
Nematomorph					3
Tardigrada					11
Arthropoda	Chelicerata	Pycnogonida			9
		Arachnida		Opiliones	22
				Scorpiones	86
				Solifugae	66
				Pseudoscorpiones	65
				Ixodida	51
				Mesostigmata	705
				Trombidiformes	1500
				Sarcoptiformes	1158
				Araneae	906
				Amblypygi	1
	Myriapoda	Chilopoda			43
		Symphyla			2
		Diplopoda			50
	Crustacea	Branchiopoda			17
		Maxillopoda	Thecostraca	Ibliformes	1
				Lepadiformes	10
				Scalpelliformes	3
				Sessilia	29
			Copepoda	Calanoida	56
				Cyclopoida	17
				Noctilucales	1
				Polyarthra	3
				Siphonostomatoida	2
				Monstrilloida	1
		Malacostraca	Hoplocarida	Stomatopoda	31
			Eumalacostraca	Amphipoda	41
				Isopoda	88
				Cumacea	1

Table 1. *Cont.*

Phylum	Subphylum	Class	Subclass	Order	N
				Decapoda	506
	Hexapoda	Collembola			286
		Protura			4
		Diplura			2
		Insecta		Archaeognatha	6
				Zygentoma	20
				Ephemeroptera	29
				Odonata	102
				Orthoptera	426
				Phasmida	6
				Plecoptera	20
				Dermaptera	23
				Mantodea	45
				Blattodea	54
				Psocodea	36
				Thysanoptera	290
				Hemiptera	3602
				Hymenoptera	6425
				Strepsiptera	6
				Coleoptera	6957
				Neuroptera	177
				Raphidioptera	4
				Trichoptera	135
				Lepidoptera	5018
				Diptera	3302
				Siphonaptera	117
				Mecoptera	1
Bryozoa					15
Annelida					155
Mollusca					598
Gastrotricha					3
Platyhelminthes					56
Rotifera					382
Acanthocephala					30
Total					**37,488**

Insects are the most species-rich class with at least 26,800 known species for the country. In recent decades, our knowledge regarding insect diversity within Iran has exponentially increased [93]. This taxon has some highly diverse orders, i.e., Coleoptera with ca. 6950 species, e.g., [94–96]; Hymenoptera with ca. 6420 species, e.g., [97–99]; Lepidoptera with ca. 5018 species, e.g., [57,100,101]; Hemiptera with ca. 3600 species, e.g., [76,102,103]; and Diptera with ca. 3300 species, e.g., [104–106] (see Table 1; a full list of references and numbers of known species in each family and order is provided in SI S1 and S2). While there are several comprehensive catalogs on some taxa, e.g., lepidopterans [57], arachnids [70], and odonates [73], no catalog is available for many large taxonomic groups at the order level, such as Coleoptera, Hymenoptera, and Diptera. Even though we reviewed the most updated lists of nearly all taxonomic groups and cross-checked the data while consulting with the known specialist of each group, the presented number of known species in this study is probably far from the real number of known species.

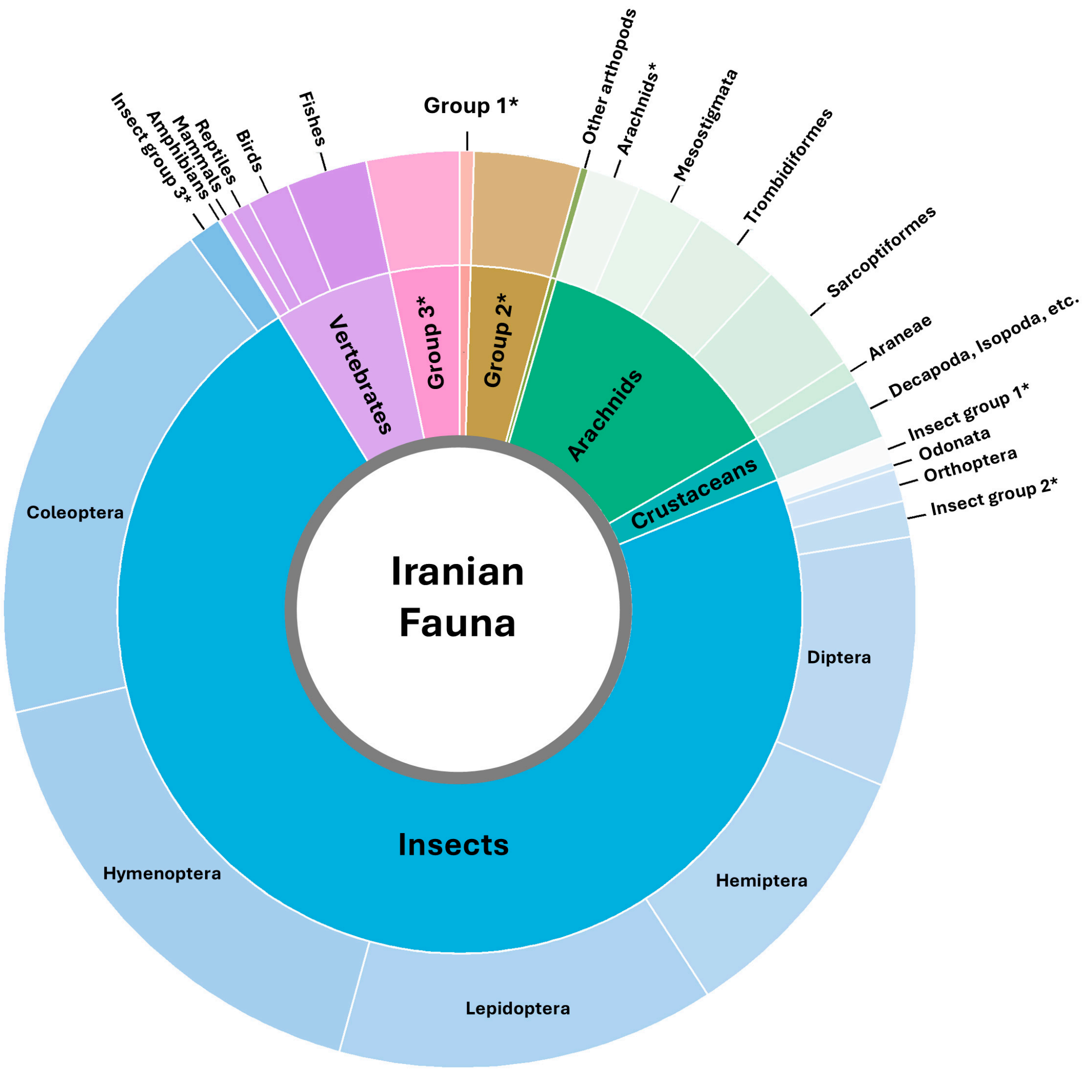

Figure 4. Proportion of species in different animal taxa for Iran. Overall, 94.4% of the species in our dataset belong to invertebrates, while only 5.6% are vertebrates. Insects include 72.3% of all the species in the country, of which 18.5% belong to Coleoptera, 17.1% to Hymenoptera, 13.4% to Lepidoptera, 9.6% to Hemiptera, and 8.8% to Diptera. Other diverse groups are Trombidiformes (4%), Sarcoptiformes (3%), fishes (all Agnatha, Chondrichthyes, and Osteichthyes; 2.8%), Araneae (2.4%), and Crustacea (2.1%). Group 1*: Ctenophora, Porifera, Placozoa, Cnidaria, Myxozoa, Cephalochordata, and Tunicata (0.5%); Group 2*: Echinodermata, Chaetognatha, Nematoda, Nematomorpha, and Tardigrada (3.7%); Group 3*: Bryozoa, Annelida, Mollusca, Gastrotricha, Platyhelminthes, Rotifera, and Acanthocephala (3.3%); Arachnids*: Opiliones, Scorpiones, Solifugae, Pseudoscorpiones, and Ixodida (0.7%); Insect group 1*: Collembola, Protura, Diplura, Archaeognatha, Zygentoma, and Ephemeroptera (0.9%); Insect group 2*: Phasmida, Plecoptera, Dermaptera, Mantodea, Blattodea, Psocodea, and Thysanoptera (1.2%); Insect group 3*: Strepsiptera, Neuroptera, Raphidioptera, Trichoptera, Siphonaptera, and Mecoptera (1.2%).

In a recent catalog of the Lepidoptera of Iran, Rajaei et al. [57] listed 4812 species in this order. However, following the comparison of the number of the two well-known groups of Lepidoptera of Iran (Papilionoideae and Zygaenidae) with the fauna of Europe and other parts of the world, Landry et al. [107] estimated that more than 50% of Lepidoptera species are waiting to be discovered in Iran. Even a cursory view of the number of recorded species in other countries can highlight the limited knowledge regarding the richness of invertebrates in this country. For instance, Völkl et al. [108] estimated the presence of more than 33,000 species of hexapods in Germany, which roughly comprise 70% of all fauna. Nevertheless, Iran is roughly four times larger than Germany, boasting a significantly greater diversity of climates and habitats [13,16]. Therefore, the represented number of species in this study probably covers only a fraction of the real diversity, and further studies are required to address the ultimate number of species in Iran.

4. Faunal Diversity Patterns

4.1. Zoogeographical Patterns

The geographic and climatic setting of a region represents the prerequisite for its biodiversity and is apparently the main determinant of biogeographic structures [3,4,109]. Iran has been recognized by researchers as a zoogeographical transition zone [15,58], as indeed the country is located at the intersection of three of the global zoogeographical realms, Palearctic, Saharo-Arabian, and Oriental [3,4]. 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 Iranian basins belong to the Saharo-Arabian realm. The arid regions of the southeastern edge of the country represent the westernmost portion of the Oriental realm [3,4] (Figure 1a). Such transitional geographic position is also evident from the complex mixture of taxa belonging to different biogeographic regions, e.g., Palearctic species like Red deer (*Cervus elaphus*), Roe deer (*Capreolus capreolus*), Brown bear (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), European green woodpecker (*Picus viridis*), Tawny owl (*Strix aluco*), and Meadow viper (Vipera eriwanensis); Saharo-Arabian elements such as gazelles (*Gazella subgutturosa*, *G. bennettii*, *G. gazella*), Cheetah (*Acinonyx jubatus*), Sand fox (*Vulpes rueppellii*), Desert cobra (*Walterinnesia aegyptia*), and Black-striped hairtail (*Anthene amarah*); and Oriental representatives like Asiatic black bear (*U. thibetanus*), Palm squirrel (*Funambulus pennanti*), Indian crested porcupine (*Hystrix indica*), Persian Krait (*Bungarus sindanus persicus*), Bay-backed shrike (*Lanius vittatus*), Sykes's nightjar (*Caprimulgus maharattensis*), Striped Pierrot (*Tarucus nara*), and Baphomet moth (*Creatonotos gangis*) [55,63,64,66,101,110].

Generally, the Zagros Mountains, extending from the northwest of the country toward the south, and in parallel with that the Ghohrud Mountains, in the margin of the Central Iran basins, limit the distribution of Palearctic elements toward the extent of the Saharo-Arabian and Oriental regions in the south of Iran. This pattern can be seen in some taxa such as the Eurasian magpie (*Pica pica*) [63] and some Geometrid moths (e.g., *Xanthorhoe wiltshirei* and *Pingasa lahayei*) [57], which are distributed in the Palearctic realm but have their most southern distribution in Iran. Conversely, some butterfly species (e.g., *Ypthima bolanica*, *Catopsilia florella*, and *Colotis danae*) with Saharo-Arabian affiliation are limited to the northern seashores of the Persian Gulf, and their distribution seems to be limited towards the north by the Zagros Mountains [101].

Its specific geographical position and unique topographical, climatic, and habitat diversity make Iran an interesting target for phytogeographic and zoogeographical studies. Hence, the use of faunal distribution data for assessing the biogeography of Iran has a long history [111]. In fact, in the same year that Alfred R. Wallace wrote his opus on the geographical distribution of animals [112], which established biogeography as a scientific subject [113], 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 [114] (Figure 2c). Further studies followed, but unlike phytogeography [115] (Figure 2d), which largely followed the three main macro-bioclimatic zones (Temperate, Mediterranean, and Tropical) identified by Djamali et al. [13], zoogeographers failed to find any consistent pattern. Blanford [114] 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 (Figure 2c). Years later, ref. [116] classified the bird fauna of Iran into nine zoological zones, whereas Scott et al. [117] recognized only eight main regions for birds. The Iranian freshwater ichthyofauna has been categorized into nineteen main basins [118], and thirteen zoogeographical regions have been identified for reptiles by [119].

In invertebrates, only a few preliminary biogeographical studies are available. Naumann [120] studied the geographic distribution patterns of the genus *Zygaena* in the Middle and Near East. Dubatolov and Zahiri [110] and Matov et al. [100] conducted more detailed biogeographical analyses to assess the distribution patterns of tiger moths (Arctiinae) and heliothine moths (Noctuidae), and [110] suggested three main territories, namely, western, northern, and central regions, that are mainly occupied by Palearctic faunal elements, whereas the northern seashores of the Persian Gulf are inhabited by Paleotropical elements (e.g., *Utetheisa lotrix* and *Argina astrea*), and the most southeastern parts by Oriental species (e.g., *Creatonotos gangis*). Dinerstein et al. [121] 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 the Baluchestan region). This zoogeographical pattern somehow indirectly reflects the global ecoregions recognized by [16], 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), ref. [122] identified three main biogeographic regions and thirteen 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, mostly without using qualitative approaches, and yielded very incongruent results. Yusefi et al. [15], however, applied two different analytical approaches, including conventional hierarchical clustering based on species turnover [123] and a novel network-based *infomap* algorithm [124] on the distribution data of 186 terrestrial mammals. The results of these studies showed good agreement in bioregionalization between the distance-based and network-based methods. Yusefi et al. [15] detected seven bioregions using a network-based method, namely, (1) Alborz-Zagros-Kopet Dag, (2) Central Basin, (3) Baluchestan-Khorasan, (4) Persian Gulf Shores-Khuzestan, (5) Makran Mountains, (6) Turkmen Plain, and (7) Makran lowlands; and two transition zones (Abarkooh–Shahreza ridges and Arvand–Shadegan lowlands). This transition zones can be considered as potential contact zones between zoogeographical realms across at the intersection between bioregions and a sharp gradient shift between Mediterranean and tropical microclimate region in this area [13,125,126]. This border has been already defined for plants (Figure 2d; between Irano-Turanian and Nubo-Sindian) [115,127] and ecoregions (Zagros Mountains Forest Steppe and Nubo-Sindian) [16].

4.2. Phylogeographical Patterns

Looking at genetic data, patterns become even more finely scaled. So far, only few genetic data are available, and the few available studies are fragmentary, mostly based on a single or a few species and genetic markers; see, e.g., [41,128,129]. 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., [58,130], and second, the important role various regions of the country as glacial refugia during the Pleistocene, e.g., [58,129,131].

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., [130,132]. 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) [133]. The barrier effect between Afro-Arabia/Mesopotamia and the Central Iran basins 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 [128]. The researchers 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 Mountains in the north (about 6.6 MYA) at the border between the upper Miocene and the Pliocene. Ghaedi et al. and Mouthereau et al. [130,134] found the same pattern in the diversification of two species in the genus *Saara* from the central Iranian Plateau (*S. asmussi*) and Mesopotamia (*S. loricata*), which were separated by orogeny events in the Zagros Mountains starting during the Pliocene. On the other hand, the Alborz Mountains act as a corridor for sharing faunistic elements between 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 [135,136].

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 refugium, which led to the long-term isolation of different species from northern latitudes and western longitudes. This is, for example, the case for the Satyrine butterfly (*Proterebia afra*) [137], the Black alder (*Alnus glutinosa*) [138], the Meadow grasshopper (*Chorthippus parallelus*) [139], the Honeybee (*Apis mellifera*) [140], the Domestic mouse (*Mus musculus*) [141], and the Cynipid gall wasp (*Synergus umbraculus*) [50]. 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 [142]. 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 [142]. The analysis of mtDNA showed very low divergence within *L. dispar* across most of the native range except for specimens from the Alborz and Zagros Mountains, 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 [143]. Similarly, the genetic analysis of a cosmopolitan Weevil pest (*Hypera postica*) revealed high diversity and a potential origin in northwest Iran [144,145].

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 the Hyrcanian Forest as a glacial refugium comes predominantly from palynological data [46,146] and phytogeographic studies [147]. However, this area has also been reported as a refugium for several faunal elements, including the Persian medical leech (*Hirudo orientalis*) [148], the Tree frog (*Hyla orientalis*) [149], the Freshwater crab (*Potamon ibericum*) [150], the Caucasian pit viper (*Gloydius halys caucasicus*) [135], and the Fat dormouse (*Glis glis* (currently *persicus*)) [51]. This is partly because of the eustatic changes in the Caspian Sea (a remnant of the Tethys Sea) during the late Cenozoic that had a great influence on the paleogeography of the region [150]. Besides being a refugium, this region shares several faunal elements with two neighboring areas in the northwest (Transcaucasia and the South Caucasus) and northeast (the Turkmen Plain and the Kopet-Dag Mountains). Furthermore, the northeastern regions harbor some unique faunistic elements and share some taxa with Central Asia [73]. Some taxa showed higher diversification and haplotype turnover in these two regions [51,135,151].

Besides the important role of the Alborz and Zagros Mountain 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 also been suggested that some isolated mountains in the Central Iran basins, particularly in Kerman and Yazd with elevations higher than 4000 m, acted as distinct islands of biodiversity surrounded by desert [122,152]. These mountains with a high rate of endemism (see, e.g., [60,62,153]) have already been mentioned as distinct zoogeographical regions by some authors, e.g., [15,116], and have been suggested as potential refugia for some species during the glacial periods (e.g., planthoppers (Fulgoromorpha), [122]).

5. Future Directions in Biodiversity Research

5.1. Lack of Knowledge

Despite being far from complete, the currently available knowledge of the vertebrate fauna and its distribution patterns is useful to draw biogeographical inferences. However, our knowledge of the invertebrate fauna is still fragmentary and insufficient [57]. There are some recent advances in updating the catalogs of Iranian invertebrates, e.g., [57,70,72]. However, there are no 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 particularly important considering the high conservation demands of many regions as anthropogenic pressure constantly rises, threatening unique biodiversity communities [59,154]. Hence, there is an urgent need to perform more systematic faunal surveys, especially for invertebrates, to understand their diversity and distributions, and to be able to more effectively protect not only vertebrate diversity but also the regions with high insect diversity. For this, more taxonomic and faunistic studies are required, which should be further supplemented with DNA barcoding data to provide a comprehensive basis for future conservation management.

5.2. Lack of Comprehensive Taxonomic Inventories and Taxonomists

Although species have long been considered the basic units of biodiversity [155], 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 highly diverse group like Arthropoda, the most diverse group of organisms in the whole history of life [156], and a country of incredibly high arthropod biodiversity, such as Iran, where our taxonomic knowledge is a long way from being complete. 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 [157] and to questionable homology assessments. On the other hand, the number of experienced taxonomists is decreasing [158,159] for many groups of organisms. This is a major dilemma not only for taxonomy, but also for any related field (e.g., ecology, biogeography, and conservation biology), especially in the epoch of the Anthropocene, when biodiversity is dramatically declining.

5.3. Lack of Comprehensive DNA Barcode Reference Libraries

While there is a lack of taxonomic and faunistic data on invertebrates in Iran, such lack 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 [160]. These DNA database archives are curated and publicly available on BOLD, the Barcode of Life Data Systems [161]. 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.

Currently, 12,748 specimen records from Iran are 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 (i.e., contain both COI-5P and COI-3P fragments; as of January 2023). In total, arthropods cover 54% of the barcode data, followed by vertebrates (27%; Figure 5). This dataset contains 11 phyla, 32 classes, 144 orders, and 10,057 genera. Globally, more than 619,794 BINs (Barcode Index Numbers) [162], 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 2297, representing 3167 described species and 14,498 specimen records that are deposited in 149 institutions. Considering that more than 1000 species of spiders and almost 5000 species of butterflies have already been recorded for Iran, the lack of comprehensive data is more than evident. More taxon-specific local studies, or even better a nationally coordinated activity, such as those in Canada or many European countries, are needed to close this gap in the future.

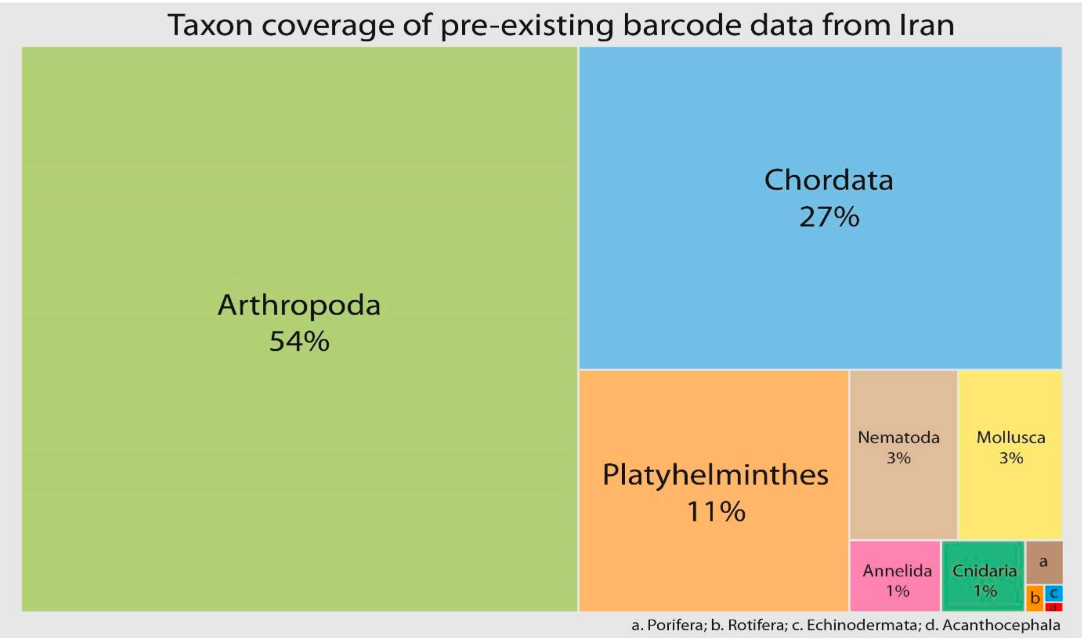

Figure 5. Taxon coverage for 11,796 pre-existing COI (including DNA barcode region) records of Iranian fauna in public DNA repository databases (BOLD and GenBank).

After assembling DNA reference libraries for the major lineages of 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.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16100621/s1, S1: A full list of the utilized references in this study for synthesizing faunal diversity in Iran; S2: A table with detailed information on species diversity at order and family level for fauna of Iran.

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