The Biogeographic Characteristics of the River Basins of Greece

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Abstract Biogeographic regionalizations provide frameworks for a holistic understanding of river basin areas and their inland water ecosystems. Here we employ the freshwater ecoregion concept to outline biogeographic aspects of the aquatic and semiaquatic biota and river ecosystems in Greece. Emphasis is given to freshwater fishes which cannot readily disperse over mountain watershed barriers and marine areas; they are utilized as primary biogeographic indicators. Although various biogeographic regionalization maps are surveyed, the Freshwater Ecoregions of the World (FEOW) initiative is adopted, and this review helps redefine certain recently published ecoregional boundaries in Greece. Along with freshwater fishes, other animal and plant distributions and knowledge of geological history and climatic patterns help guide the boundary definition of eight freshwater ecoregions in Greece. Gaps in knowledge concerning species distributions and taxonomy as well as the biogeographic understanding of each freshwater ecoregion are assessed.

Keywords Aquatic biota, Conservation, Freshwater biodiversity, Freshwater ecoregions, Freshwater fishes

Contents

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1 Introduction

River basins are virtually “biogeographic islands” for freshwater biota. At a regional spatial scale, large areas with aquatic ecosystems that share species assemblages can be described as “ecosystem regions” or ecoregions. Robert Bailey [1], who championed in ecoregional cartography, defined ecoregions as “major ecosystems” ... “resulting from large-scale predictable patterns of solar radiation and moisture that, in turn, affect the distribution of local ecosystems and their component plant and animal species.” For the realm of inland water ecosystems, these regional entities are appropriately termed freshwater ecoregions [2], and they have become key geographical units for aquatic ecosystem inventories, monitoring, and conservation planning in recent years [3]. Ecoregions are also important conceptual frameworks to describe and evaluate a country’s biodiversity and natural aquatic resources.

Ecoregional classifications have been widely used as a first-tier screening in procedures for classifying water resources, and they are also a key geographical criterion for river typologies within Europe’s Water Framework Directive – WFD 2000/60/EC [4]. Many researchers have called for a hierarchical river classification, where a regional or ecoregional typological criterion tops the standardized classification framework (e.g., [5, 6]) (Fig. 1). In 2008, a global assessment to delineate the Earth’s freshwater ecoregions was promoted by conservation organizations [8, 9].

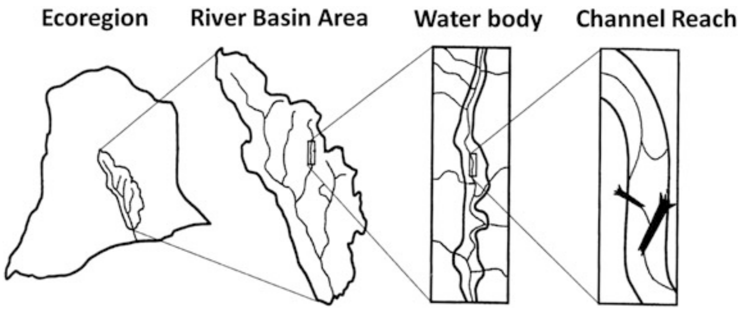

Fig. 1 Scales of river classification that are now part of policy-relevant river management, conservation planning, and monitoring; ecoregions or other biogeographical regions top the hierarchy (adapted from [6] as presented in [7])

This project produced practical classification and regional delineation criteria and a first baseline charting freshwater ecoregions on a global scale.

The Freshwater Ecoregions of the World (FEOW) project is primarily a freshwater biogeography scheme. It is guided by the influences of freshwater species' phylogenetic history, paleogeography, and ecosystem distribution patterns in order to delineate regions exhibiting relative homogeneity of aquatic ecosystem structure [8]. This regionalization mainly utilized freshwater fish species distributions as proxies for the distinctiveness of wholly aquatic biotic assemblages [3]. FEOW utilized watershed lines and deep marine waters as criteria for boundaries, unlike the older "terrestrial" ecoregional schemes which give overriding value to potential natural vegetation and general physiographic and climatic characteristics [10–12]. Expert judgment was important in making final boundary decisions and a prestigious panel of biodiversity experts contributed to the freshwater ecoregion delineations [9].

Regionalization schemes such as ecoregion mapping show varying scales of regional analysis. The freshwater ecoregional scale is definitely spatially restricted relative to the much broader "biome" scale or the recently redefined "major zoogeographical region" scale [13]. For the smallest freshwater ecoregional units, it is difficult to define a size limit; they usually extend for several hundreds of kilometers and often include at least several dozens of more or less biotically similar river basin areas (i.e., a simple rule of thumb being that "each basin is a state, each ecoregion a country"). However, in exceptional cases there are some rather small freshwater ecoregions, such as some very large tropical lake systems and large islands which are characterized by millions of years of isolation and outstanding evolutionary divergence [2]. Greece, for example, is a country on a "biogeographic crossroads" where rather small ecoregions meet. The territory of Greece includes eight freshwater ecoregional units, the largest number of ecoregions of any EU country (Fig. 2).

In this chapter, we explore the biogeographic ecoregions that encompass Greece's river basin areas, and we survey and interpret the FEOW ecoregional delineations. Controversy and disagreements on boundaries persist, and the issue of completing an accurate ecoregional map for the freshwater realm is still in progress. After many

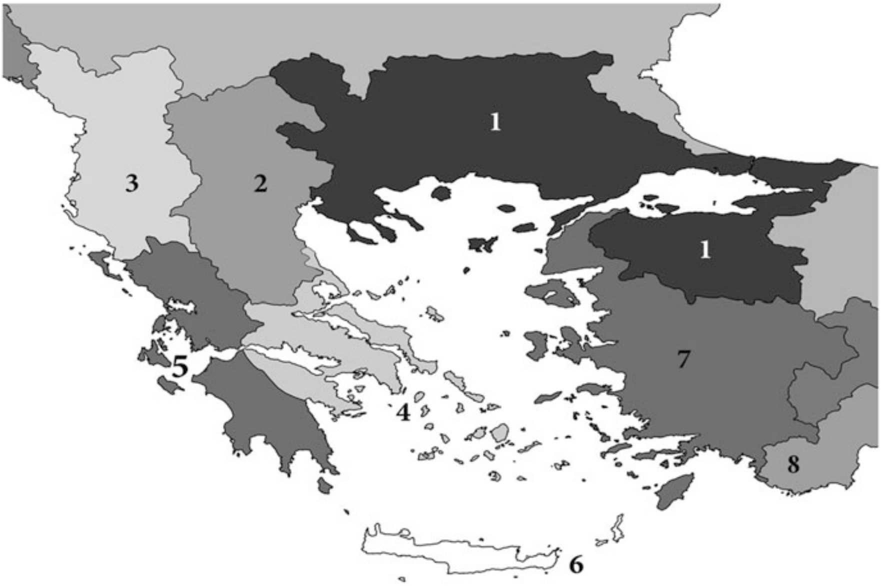

Fig. 2 The freshwater ecoregion delineations of Greece and the surrounding lands as developed by the Conservation Science Program of World Wildlife Fund and The Nature Conservancy [9]. There are still disagreements among some of the boundaries; see text (*numbers* have been superimposed and correspond to Table 1). Map extracted from FEOW [9]

years of working with the ecoregional framework at the Hellenic Centre for Marine Research (HCMR), we propose specific boundary changes to the FEOW map and we document them, but this is not the place to do this exhaustively. Although we use the relevant biogeographic literature and previous fish-based biogeographic analyses, we do not dwell on describing the historical biogeography in detail (i.e., interpreting biogeographic dispersal episodes or routes or the genesis of current biotic assemblages). The ultimate goal here is an introductory regional-scale review of freshwater lotic ecosystems and their biota.

2 Previous Biogeographic Delineations

Due to its remarkable position among three continents and its diverse and fragmented mountain chains and archipelagos, Greece has been a focus area for biogeographic research (e.g., [16, 17]). However, the overwhelming majority of research has focused on terrestrial biogeography; terrestrial species of plants and animals on the islands have dominated biogeographic work for long periods [18–20]. The Aegean is one of the world's hotspots for island biogeographic research, and many new theoretical and analytical approaches and interpretations have been produced in this area [21–24]. This biogeographic research has also helped to integrate a huge body of literature from various research endeavors, including geology, paleontology, archeology, climatology, botany, zoology, ecology, and conservation science. Biogeography is particularly important for exploring systematics and taxonomy, especially in areas where species have evolved in isolation or retained relic populations. As a result of decades of biogeographic research, many disparate biogeographic maps have been published, using very different indicator taxa groups (e.g., terrestrial invertebrates, reptiles, the paleofauna, endemic terrestrial flora, potential natural vegetation, etc.).

Botanists have contributed significantly to biogeographic regionalizations in Greece. Turrill [19] in 1929 was the first to divide the country into six phytogeographical regions. Later, Rechinger (1943) [18] first addressed the phytogeographical peculiarities of the Aegean and discovered the important biogeographic boundary along the mid-Aegean trench, known now as "Rechinger's line" – the biogeographic divide between the European and Asian Aegean [17]. Ganiatsas [25] also produced a phytogeographical map based largely on Rechinger's work (Fig. 3a). Some years later, Strid [17] divided Greece into 13 phytogeographical regions, and this practical compartmentalization, also based on the previous phytogeographical regionalizations, has remained unchallenged and is widely used today [27, 28].

The zoologists also charted biogeographic boundaries in Greece. Often these "zoogeographical maps" were exclusively for specific taxonomic groups, including on some occasions freshwater aquatic and semiaquatic groups (Fig. 3b, c). Distributional knowledge of the amazing array of arthropod diversity in Greek aquatic ecosystems is limited in part because of the lack of local taxonomic specialists and the relatively late beginning of taxonomic studies. It should be pointed out that by the late 1970s and early 1980s, zoogeographic interest in Greece helped establish the International Congress on Zoogeography of Greece and Adjacent Regions (ICZEGAR) first promoted by Prof. I. Matsakis and by many "philhellene" European biologists who had been collecting biological material throughout Greece. ICZEGAR is still a hive of development for biogeography in Greece and the wider region [29].

Regarding aquatic animals, freshwater fishes dominate biogeographic research in Greece. We owe a lot of baseline work to Prof. PS Economidis, an

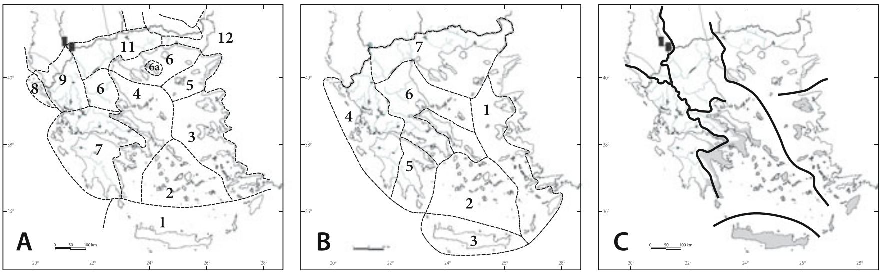

Fig. 3 Important biogeographical delineations for various biotas: (**a**) Plants [25]; (**b**) *Hydraenidae* beetles [26], and (**c**) major freshwater biota assemblage breakpoints (key barriers to dispersal) mainly using fish distributions (this study); *gray-colored areas* in map (**c**) show areas where intermittent and ephemeral stream flows dominate lotic waters, due to seasonally semiarid conditions and geology (adapted from [7])

intrepid explorer who collected and collaborated with many ichthyologists since the late 1960s (e.g., [30, 31], and references therein). However, most modern fish-based biogeographic maps are either rather repetitive or their boundaries vary with respect to changing species taxonomies (nomenclatural changes) and species subsets utilized in the analyses (e.g. [32–34]). Different spatial scales in the regionalizations also influence biogeographic boundaries; broadscale applications necessarily create unconventionally much larger and fewer regional units (e.g., the Europe-wide analysis of Reyjol et al. [35]). In recent ichthyogeographic delineations, only the most prominent boundaries resulting from the river basin fish assemblage classification analyses are charted, and specific criteria for boundary setting are set [36, 37], while more sophisticated quantitative methods are applied (e.g., [38, 39]).

Compared to fishes, there is limited work on other freshwater biota in Greece or the neighboring Balkan and Asian countries. At the continental scale, with respect to the European freshwater biota, spatially broad and rather crude freshwater biogeographic regional delineations were originally proposed by J. Illies [40] in his multi-taxa freshwater zoogeographical compilation *Limnofauna Europaea*. However, Illies's freshwater ecoregions have been seriously criticized and are now considered outdated and partially flawed [36]. Despite this dispute, Illies' boundaries were used for partitioning European ecoregions for Europe's Water Framework Directive [4] inland water typologies. One reason for the difficulty of producing freshwater ecoregional maps has been the many varied and disparate distributional patterns of very different "freshwater" biota; some taxa are wholly aquatic, large-sized poor dispersers (such as mussels), while many are semiaquatic or can even disperse terrestrially by flying across biogeographic barriers (i.e., many semiaquatic insects). A major problem with aquatic invertebrate work is that inventories and distributional surveys for many species are incomplete or poorly surveyed [41, 42].

Biogeographic ecoregion regionalizations have thus encountered controversy; different spatial scales, statistical methods, and methodological delineation procedures are used, and many biogeographic maps of the same area give quite different boundaries. For example, Illies's [40] biogeographic maps based on many animal taxa were altered with different published editions and later politically relevant usage within the WFD, i.e., using state borders instead of biogeographic characteristics (Fig. 4).

Aquatic biogeographic cartographers look for common biotic breaks in species distributions in order to chart regional boundaries. For example, the concept of faunal break boundaries refers to specific boundary lines of rapid faunal change that are usually associated with prominent long-standing geographical, geological, marine, and/or climatic barriers to species dispersal, such as watershed lines; see Fig. 3c. Faunal break boundaries are obviously scale dependent, and the degree of dissimilarity will vary based on taxonomic groups used, their dispersal abilities, and several other parameters. Misinterpretations or differing opinions easily get published [36].

Fig. 4 Gradual changes in the broadscale freshwater zoogeographic "ecoregions" of Illies's *Limnofauna Europaea* (the first two maps from the *left*, with published volume dates) and the final ecoregion map used in the Water Framework Directive [4]. For ecoregion names, *numbers* are provided in Table 1 (figure redrawn from [7])

Finally, we should mention that regional syntheses based on terrestrial ecoregional concepts are probably even more difficult to standardize than the freshwater biogeographic approaches, since even more parameters are introduced to the "ecoregional" perspective [10, 43]. Since distributional patterns of many freshwater taxa and the ecosystem processes that sustain them do not usually correspond well to terrestrial ecoregion boundaries, we endorse the development of separate freshwater and terrestrial frameworks for conservation-based analyses [2].

Generally, modern terrestrial ecoregional maps vary among scientific teams and subdisciplines, and this has sometimes created confusion [44]. A recent conservation-relevant procedure focused on terrestrial ecoregions of the world [11, 45] using potential natural vegetation categories and various species distributions among other criteria (Fig. 5). The authors of this map do warn that "no single biogeographic framework is optimal for all taxa and ecoregions reflect the best compromise for as many taxa as possible" [11]; boundaries rarely form abrupt edges but are bound by ecotones and mosaics. Our opinion is that this work is a gross generalization and does not compare well with the diversity of other potential natural vegetation renditions in Southeast Europe [46] or even traditional biogeoclimatic cartography [47] for the region. Olson et al.'s [11] global terrestrial ecoregional map was significantly revised in some parts of the Earth's surface (i.e., Arabian Peninsula) in its reissue in 2017 [45], but the ecoregional delineations in the Balkans remain unchanged. Nonetheless, the conservation-relevant gap analyses using this map have produced a very useful global conservation evaluation [45].

3 Geological Setting

Greece exhibits a unique geophysical diversity and a tumultuous geological history in its 132,000 km^2 area. It has over 3,000 islands, and if we include islets and rock stacks, the number surpasses 7,800 islands and islets [48]. Greece is also a land of

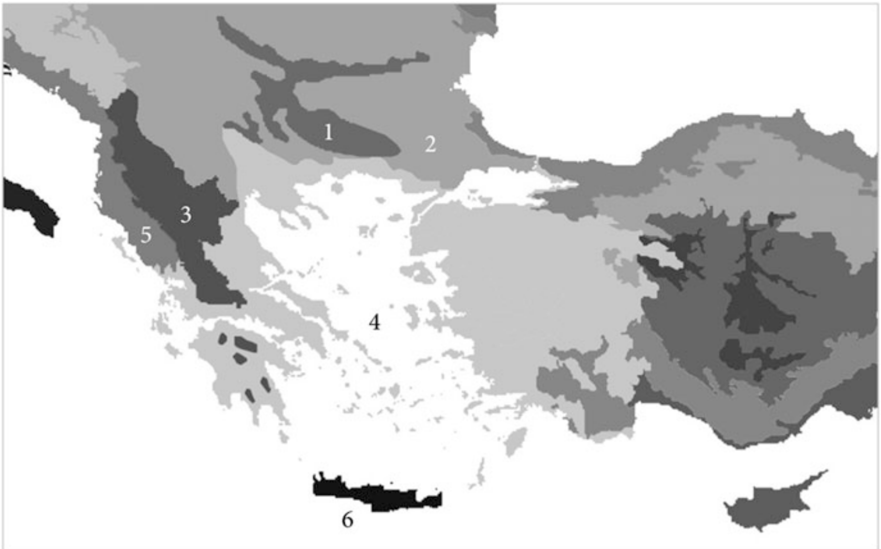

Fig. 5 Segment of the terrestrial ecoregions of the world map by Dinerstein et al. [45]. Six ecoregions are delineated in Greece's territory: (1) Rhodope montane mixed forests, (2) Balkan mixed forests, (3) Pindus mountains mixed forests, (4) Aegean and Western Turkey sclerophyllous and mixed forests, (5) Illyrian deciduous forests, and (6) Crete Mediterranean forests. Extracted map adapted from Dinerstein et al. [45]

hundreds of peninsulas. Although only about 20% of the land area is made up of islands and islets, there is a uniquely convoluted and incredibly long coastline with hundreds of autonomous river basin areas. An overwhelming number of river basins are very small; many small non-perennial streams and torrents dominate in the islands, peninsulas, and dry coasts. In contrast, some sizable rivers, including large transboundary basins, exist in the northwest and north. This globally unique geographical configuration is a result of the tectonically active geology of the southern Balkans and its surrounding regions [49, 50].

The geological history of the Balkans and the Aegean region is complex, involving dynamic tectonic action and long periods of orogenesis that created an evolving geographical scene effecting the distribution and diversity of the freshwater biota. As outlined by Bănărescu [14] and Skoulikidis et al. [51], the following main attributes seem to be the major geological events that produced such complex biogeographic patterns in the freshwater biota of the southern Balkans:

1. The existence of the former Tethys Sea (in the region between the current Mediterranean-Danube Valley-Black Sea-Caspian Sea).
2. The orogenic upheaval of the Carpatho-Balkans separating the wider Tethys into a southern (Mediterranean) and northern sector, the Paratethys, much of which later formed large lakes or dried out.

3. The orogenic upheaval of the long and narrow Pindus cordillera (an extension of the Dinaric Alps) separating Greece and the Western Balkans into east-west biogeographic sectors.
4. The existence of many ancient lakes, many derived from various parts of the Tethys and Paratethys, which host many long-isolated endemic species.
5. Fluctuations of sea levels in the Adriatic enabling faunal exchange between Italy, the Northern Adriatic and the Western Balkans.
6. The continental contact and separation between the southern part of the Balkans and Anatolia: until the beginning of the Middle Miocene, the southern Balkans and Asia Minor comprised a continuous composite landmass (Fig. 6a); this was interrupted by the Aegean landmass subsidence during the late Miocene (Fig. 6b).
7. The existence of archipelagos due to remarkable tectonic diversity and volcanism in the Aegean, including the creation of a distinct southern island mass (Crete) (Fig. 6c).
8. The desiccation of the Mediterranean at several periods, but especially during the Messinian Salinity Crisis (from 5.96 to 5.33 MYA), which favored freshwater flows and connections among formerly disjunct river basins.
9. The Pleistocene glaciations which dropped eustatic sea levels down to approximately 120 m and created connections among many river basins (Fig. 6d) but also created climatically benign "refugia" in the southern coastal and lowland parts of our area.
10. The gradual modification of river networks through repeated river captures (river piracy in tectonically active areas) which blended the headwaters of rivers and helped biota dispersal over previously impenetrable mountain watersheds.

4 Climate

The Mediterranean climate was established about 3.2 MYA [53], and during the Holocene, most of the territories belonging to Greece have been typically Mediterranean in climate. The Mediterranean climate is diverse, and there are important variants that affect the water cycle, hydrological flow regimes in surface waters, and the aquatic communities. Precipitation is irregularly distributed across Greece, ranging from 1,300 mm annually in northwestern Greece (especially in the Tzoumerka mountains) to 300 mm in the southeast coastal rain shadow areas [54]. The west side of Greece, west of the Pindus mountain range, is much wetter and more humid than the eastern part. In much of eastern continental Greece, rain shadow areas create pockets of seasonally arid conditions with high evapotranspiration rates and a long summer drought. These rain shadows create conditions where non-perennial river systems dominate, since long-term droughts define the character of flow regimes [55]. Hydrology and natural flow regimes vary remarkably among basins and longitudinally along the river courses, depending on local climate and the geological,

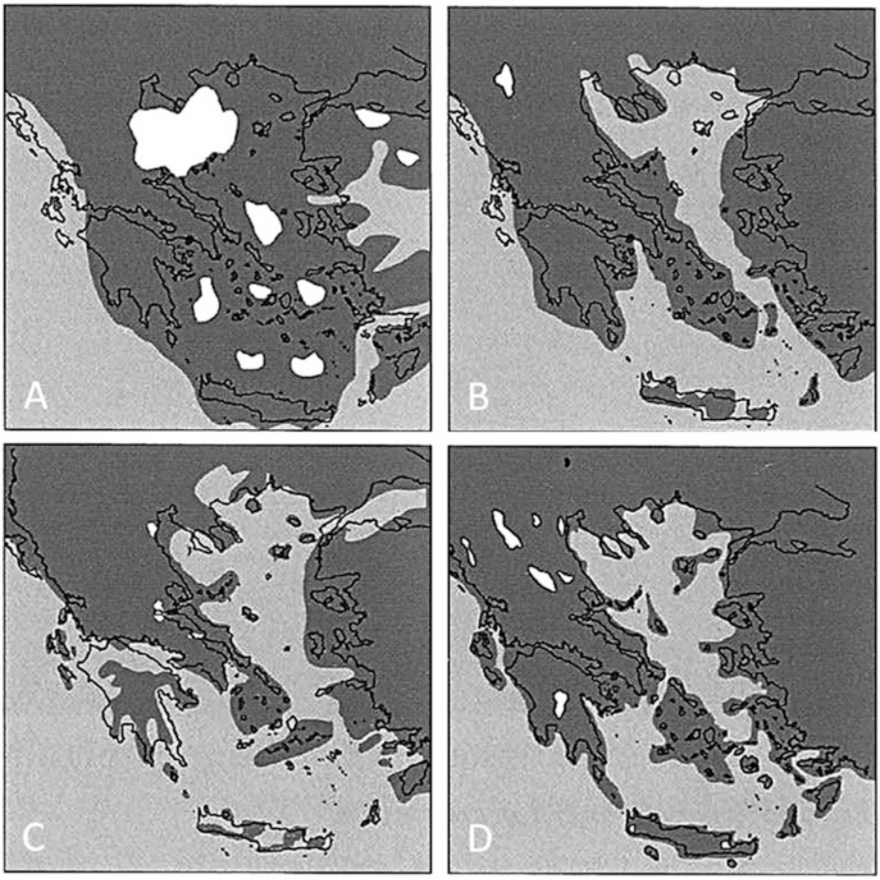

Fig. 6 Examples of paleogeographic change in Greece: landmasses in *dark gray*, lakes in *white* (the present geography outlined within the images). (**a**) Middle Miocene 12 MYA, with the Aegean being a continual landmass; (**b**) late Miocene 8 MYA, first breakup of the Aegean; (**c**) Pliocene 3.5 MYA; south Aegean arc islands including Cretan paleo-islands. (**d**) Middle Pleistocene 0.8 MYA; lowering eustatic water levels during glacials reconnect islands, and many river basins merge. Selected map depictions originally from Valakos et al. [52] and modified in Zogaris [7]

geomorphological, and topographical conditions. Due to the predominance of calcareous geology in western and southern Greece, karstic springs are very important in providing steady flow regimes to relatively small rivers [51]. Spring-fed streams are therefore quite incongruous "oases" and are often associated with geological patterns and a steep mountain relief. In contrast, disturbance regimes such as flash floods and severe droughts are also common, often even in small seasonally arid torrents. Climatic research has shown that important aspects that affect lotic waters and their biota in the Mediterranean are droughts, and a remarkable variability of precipitation pattern has been documented through the centuries [56]. It is certain that even before the high-intensity water exploitation of modern times, there have been "epic megadroughts" that may have had an important role to play in the locally impoverished state of insular and peninsular aquatic faunas and floras. Finally, the influence of anthropogenic water abstraction and climatic variability or recent climatic change create mixed stresses on running water ecosystems, and it is often difficult to interpret what is modified solely by human activities [57].

5 The Aquatic and Riparian Biota

The southern Balkans and Anatolia are famous as acting as biological refugia during the past glacial periods, thus conserving many Eurasian aquatic and semiaquatic species that were extirpated by climate change in much of temperate Europe. Isolation and vicariance (i.e., the splitting of populations by barriers to dispersal) have created conditions for the evolution of a large percentage of range-restricted species, known as local endemics. Endemics can be defined to a geographical entity (such as a region or the state's political borders). One of the most outstanding attributes of using biogeographic indicators is the identification of areas where these range-restricted species concentrate. The territory of Greece has the highest percentage of endemic fishes in the EU [58] and may equally be important as a center of endemism for aquatic, semiaquatic invertebrates and aquatic species parasites as well [59]. In contrast, many aquatic microorganisms are generally very widespread (cyanobacteria, fungi, and microscopic plants) since they are dispersed by atmospheric phenomena or larger animals [41]. Evidence of the cosmopolitan distribution of lentic planktonic organisms and other microscopic plants and animals has been documented in Greece [38]. Biogeographic patterns can certainly be gathered for interpretation purposes from reviewing a wide range of aquatic and semiaquatic species distributions. Below we provide a summary of some well-known aquatic species groups with notes on their usefulness as biogeographic indicators (Fig. 7).

5.1 Aquatic and Riparian Plants

Plant distributions and vegetation formations are informative for ecoregional cartography [10]. In Greece, most botanists have focused on terrestrial species, terrestrial vegetation, and particularly on the floral distribution patterns in the archipelagos and mountains [60]. Aquatic plants were less interesting for early plant biologists and collectors since most of the range-restricted species are actually dry-land species, often inhabiting rocky outcrops, mountain cliffs, etc. In fact, Greece is a global center of plant endemism for many such species groups: the country sustains 1,462 endemic plant taxa (species and subspecies) which roughly amounts to 22% of its 6,600 documented

Fig. 7 Various animal taxa that provide biogeographic knowledge. (**a**) The Freshwater crab *Potamon pelops* from the Peloponnese (Alpheios river); (**b**) unidentified unionid mussels from the Western Aegean Ecoregion (Spercheios river); (**c**) endemic *Rhodeus meridionalis* from the Macedonia-Thessaly Ecoregion; (**d**) endemic Greek stickleback *Pungitius hellenicus* and a water snail (*Theodoxus* sp.) from the Western Aegean Ecoregion; (**e**) terrestrial salamander, *Lyciasalamandra luschani* from the Southern Anatolian Ecoregion (Kastellorizo island). (Photos (**a**) I. Strachinis; (**b**) A. Christopoulos; (**c**, **d**) S. Zogaris; (**e**) K. Sotiropoulos)

taxa [27]. Most of the local endemics are in the southern part of Greece, the islands and mountains [61, 62].

Unlike the "taxonomically attractive" local endemics, the aquatic and "water-loving" (hydrophilous) plant species are geographically rather widespread. Many hydrophilous plants are easily dispersed primarily by atmospheric phenomena, migratory birds, and other animals. Recent reviews show a poor documentation of hydrophilous species (e.g., [27, 63, 64]). Some species distributions are poorly known because their aquatic and wetland habitats have suffered much change in Greece during the last century, and the smaller wetland habitats have been poorly surveyed [65, 66].

Since hydrophilous plants are particularly dependent on specific aquatic and humid habitat conditions, some species that are "intolerant" to drought (or the effects of seasonal water scarcity) have become locally or regionally extirpated. Despite their widely scattered distributions, some species groups, even such as the charophytes (macroalgae in the family *Characeae*), include taxa that are said to have localized distributions, and some are considered threatened [63]. Species that need deeper waters and stable lentic conditions in rivers, such as water lilies and water chestnuts, for example, are scarce in the southern half of the Hellenic peninsula and its islands; these are locally common in the larger river basins of the north and northwest of the country. In fact, one of the few recent plant extinctions in Greece includes a water plant, *Stratiotes aloides* (Hydrocharitaceae), which was used to be found in north-central Greece [27]. It is unusual that only a very few hydrophilous plants are featured in the Greek Red Data Book account of 2009 [28]. The Red Data Book does, however, include some interesting and rare Mediterranean endemic species such as *Callitriche pulchra* (Gavdos, Crete ecoregion) and the riparian orchid *Dactylorhiza pythagorae* (Samos, Eastern Aegean Ecoregion), but information of many important species and groups such as the charophytes is scant and poorly inventoried and documented [63, 66]. Finally, the bibliography on river plants is very limited for such a rich country in streams and the value of these plants as bioindicators (e.g., [67]).

Riparian vegetation includes all wetland and riverside or lakeside vegetation that is influenced by the adjacent water body. European assemblages are very similar to the water plants in being rather widespread. However, there are several distinct riparian plant communities with biogeographic characteristics defining particular patterns especially in Southern Europe [68] and parts of Greece [69]. Interesting and widespread riparian trees in Greece include the oriental plane (*Platanus orientalis*) and bay laurel (*Laurus nobilis*); these are relics from the Tertiary period that have long become extirpated from other parts of Southern Europe. Some very rare woody plant assemblages exist that have high biodiversity and biogeographic interest. These include river riparian stands of the oriental sweetgum *Liquidambar orientalis* on Rhodes Island and the Cretan date palm *Phoenix theophrasti*, restricted to Crete and Southwestern Anatolia. In Greece, a north-south gradient in species richness in river riparian woody plants can be detected, with northern montane assemblages being much richer in species than the south [70]. This pattern may be also due to anthropogenic degradation since southernmost areas have had much denser human populations along river valleys than the more extensive mountain areas of the north.

5.2 Aquatic Invertebrates

Although not a single taxonomic group, this is definitely the most important animal assemblage in terms of sheer biomass and species diversity in inland waters, wetlands, and riparian zones. The aquatic invertebrates include many groups such as arthropods, flatworms, worms, gastropods, bivalves, and a myriad of microscopic forms that are found in nearly all running water environments, even in intermittent or near-ephemeral stream conditions. Some of these organisms disperse among water bodies via the atmosphere (many insects for example have a flying stage); others use dispersal vectors such as birds [71, 72]. Relatively poor interbasin dispersers are the wholly aquatic benthic groups such as the bivalves [73] and several gastropods [74]. Many spring-inhabiting snails are restricted to specific parts of Greece, and many new endemic species are still being described [75–77]. Some aquatic insects such as the aquatic beetles (Coleoptera) in the family Hydraenidae also include relatively poor dispersers [26, 78], and several other beetle groups also have many range-restricted species, many endemic to parts of southern Greece [79]. Generally, it is estimated that Greece has more than 4,000 endemic invertebrate species, an incredible number for such a small country [80].

Endemicity of macroinvertebrate species seems to be highest in the south and west of the country and in the islands [81], and this is also reflected in many terrestrial invertebrates [79, 82, 83]. Prominent barriers to lowland species are the main mountain chains, especially the Pindus. In some groups such as the planarian flatworms (Genus *Dugesia*, Platyhelminthes), initial patterns of distribution are surprisingly similar to aquatic vertebrates [84]. The larger islands and peninsulas have more endemics; Crete, for example, is an important endemicity hotspot. In the southern part of Greece and the west, even widely distributed insect groups such as the dragonflies (Odonata) and stone flies (Plecoptera) have endemic species [80]. Freshwater crabs are widespread in Greek streams and rivers (species belonging to the genus *Potamon*), some considered endemic to parts of Greece. Of the crustaceans, freshwater shrimps and amphipods are also especially interesting biogeographic indicators as well [85, 86].

Lastly, general patterns also show Greece's high species richness, since many species from nearby biomes and zoogeographic regions enter the territory [87–90]. Greece is located way to the east and south on the European continent and hosts many interesting species that have their centers of origins in Asia, examples being the huge Bellostomid water bug (*Lethocerus patruelis*) which just reaches Europe solely in the extreme southeast and the damselfly *Epallage fatime* which has mostly southwestern Asian distribution.

It is remarkable that the aquatic invertebrates are still so poorly studied in Greece; even work on common and rather large-sized groups is preliminary or at a developmental stage (e.g., [42, 73, 91, 92]). Despite the outstanding importance of the larger benthic macroinvertebrates, for stream typology and ecosystem understanding, few works exist on species assemblages in specific running water ecosystem types. Several works focus on general patterns of distribution at family or genus level (e.g., [93, 94]) mainly for the purposes of ecological status assessment and monitoring. Moreover, many crenobionts – the spring-inhabiting aquatic invertebrates – show remarkable endemism, and many may be threatened with extinction [76, 95]. Unfortunately, the most recent Greek Red Data Book compilation in 2009 pays little attention to many groups of aquatic invertebrate species primarily due to the grave lack of completeness in documented distributional knowledge [80].

5.3 Freshwater Fishes

Freshwater fishes are the most widely utilized biogeographic indicators in inland waters at the regional scale, and they are rather well studied in Greece. There is much to be learned by utilizing fishes in conservation biogeography [96], and their importance as biogeographic indicators has been corroborated by historical biogeographic evidence [15, 34] and new analytical methods [97]. Importantly, fish proved to be good vehicles to explore phylogeography with new and developing genetic molecular methods and analyses [98]. Extensive collections of genetic samples that grace museum and academic archives from nearly all fish populations in our area of study and the surrounding states have been rigorously studied during the last two decades. The genetic work has assisted in making quantum leaps for taxonomic clarification and the understanding of biotic affinities among taxa and their constituent river basin areas [58, 99]. Thus, the overriding importance of fishes in regionalization work has dominated recent freshwater biogeographically based ecoregional delineations [8]. The importance of freshwater fish geographical distributions has created increasing interest in taxonomy, as has the description of many new range-restricted species, especially in endemic-rich areas, such as the Balkans and western Asia. Fishes are one of the earliest biogeographic elements explored in the Balkans [100], and interest in their distribution patterns has continued to produce many and varied fish-based biogeographic maps.

Greece is the richest country in the EU in terms of its endemic fish species and one of the most important for fish conservation in the Mediterranean [101]. At least 47 out of its 160 freshwater fish species are now considered exclusively endemic within the country's boundaries; several more taxa – at least 15 – are near endemic, i.e., confined to Greece and the near-border frontier areas with neighboring Balkan states (i.e., shared water bodies such as Prespa, Doirani, and Butrint basins). Hydrographic isolation and vicariance are the main factors responsible for Greece's ichthyofaunal diversity. Fish-based biogeographers are not only interested in the endemics; they carefully use all species that are more or less intolerant of seawater and do not disperse through the seas. Primary freshwater fishes are those with little or no tolerance of brackish water (i.e., water with more than 0.5 g per liter total dissolved mineral salts), while secondary freshwater species are tolerant of brackish waters but normally occur in inland aquatic systems rather than the sea, and some are capable of occasionally crossing narrow sea barriers [102]. Primary or primary-like freshwater fishes are by nature confined to freshwater island-like basins, and many of these species have been confined for several millions of years [33, 98]. It should be noted, however, that the arithmetic figures of endemism attributed to the country are changing almost every year as range extensions are discovered (e.g., particularly in Albania; see [103, 104]). Furthermore, the actual number of inland water fish species is also not easily determined, as various marine species are often encountered in the lower sections of inland waters, while new translocated species are becoming established in the wild, particularly in lake and reservoir systems. Finally, taxonomic changes continue taking place at a rapid pace, with new species being described, former synonyms being reinstated, and former "subspecies" validated to species rank. This dynamic state of seemingly perpetual taxonomic change may be confusing, but the situation is clearing up as detailed checklists are regularly revised [58, 105].

5.4 Reptiles and Amphibians

Terrestrial reptiles are at the forefront of zoogeographical research in Greece [16, 23]. The country hosts at least 63 reptile and 23 amphibian species, thus being particularly rich in European terms [106]. Semiaquatic amphibians are less studied, but there are very good case studies that inform biogeographic patterns [107]. Endemic amphibian taxa are confined as endemics to Crete, Karpathos, and some other areas [80]. Also as in fishes, the Pindus mountain range acts as a prominent biogeographic barrier; a near-endemic frog and some newt species, and some terrestrial reptiles, are found only along the west coast of Greece and Albania, bounded by the Pindus [52]. As are fishes, many reptiles are liable to extinction in more fragmented isolated geographical areas such as peninsulas and islands [108]. Reptile species taxonomy has seen many recent changes and much informative phylogeographic research at the genetic level, similar to the changes seen in fishes in the first years of the twenty-first century.

5.5 Birds

Birds are well studied in Greece [109]. Although they are the best interregional dispersers and many species undergo mass migrations, there are some species with distinct biogeographic regional distributions. For example, species with an "eastern distribution" are found most frequently or in larger concentrations in northeastern Greece and the larger wetlands of the Eastern Aegean islands [20, 110]. Some characteristic and iconic waterbirds are collectively near absent from the western parts of Greece (i.e., west of the Pindus range). Many species seem to be much more abundant and frequent in northeastern Greece despite the fact that adequate and extensive wetland habitats exist along the coast of western Greece, and this relates to the important land bridge migration flyways of Thrace. The long cordillera of the Pindus mountains is an important boundary that affects bird migration [109], and even certain long-distance dispersers such as pelicans are known to have different subpopulations on either side of the Pindus cordillera [111]. In rivers it is difficult to tally the full number of birds using exclusively aquatic or riparian habitats; many terrestrial species also use the waters [41]. Finally, birds and especially the waterbirds are very important for the dispersal of plants, animals, microbes, and fungi (seeds, cists, spores, etc. attached to the mud on birds' legs and feathers) [112]. A large suite of aquatic organisms can also survive passage through the digestive systems of birds because of a digestive trade-off in many birds [72]. In Greece, the north-south distribution of many widespread plant and small aquatic invertebrate species probably has its origin in bird-assisted dispersal along the north-south mass migration routes.

5.6 Mammals

As everywhere in Europe, a megafaunal collapse has taken place during the late Pleistocene and early Holocene [113]. This remarkable species turnover is outstanding in the Aegean islands, where several endemics had developed, such as dwarf elephants [114]. Crete, for example, has one of the best-studied fossil histories of mammal colonization and adaptive radiation in the Mediterranean [115]. There is now much evidence that human-induced overkill is the reason for the rapid extinction of many animals on the Greek islands [116]. During the last 2000 years, several species have gone extinct on the mainland too; these include lion, bison, aurochs, and beaver, among others [117, 118] while the Anatolian leopard may have existed on Samos until little more than a century ago [119].

Greece's extant mammal fauna is still quite rich; it includes more than 115 species [80], although large mammals are noticeably scarce. The mammal fauna of exclusively semiaquatic or semiterrestrial species is limited, but many species utilize rivers, lakes, and wetlands. The European beaver (*Castor fiber*), a keystone "ecosystem engineer" in running waters, was native in mainland Greece and is said to have become extinct in the early nineteenth century, perhaps last recorded in the Alpheios river [117, 120]. However, this is difficult to verify, and there are conflicting interpretations of past ranges and exact extinction dates for the beaver in the Balkan countries [121]. Sadly, little has been written about the beaver in the Balkans or Anatolia, and a thorough review is much needed.

Mammals disperse rather slowly and are prone to extirpation and extinction, and they are limited by recently created natural and artificial barriers to movement. Extinction rates are more rapid on islands and peninsulas, and species may go extinct with little knowledge of how and exactly when (see references to large mammals on the Aegean islands in [119]). A semiaquatic mammal once thought to be rare and geographically localized in Greece is the Eurasian otter (*Lutra lutra*). In fact, it is quite widespread in mainland Greece but is rare and perhaps declining in xerothermic areas with little permanent water, although still found even on some islands, including very small river basins on Euboea, Kerkira, Lefkada, Samos, Chios, and Lesbos islands. The species may have existed on other islands, and there is anecdotal evidence for extirpation, but this is poorly documented. Interestingly, an endemic otter species (*Lutrogale cretensis*) existed until about the late Pleistocene on Crete; the genus *Lutrogale* survives in southern Asia but had a wider distribution in the past [114]. Terrestrial mammals do show some general biogeographic trends, some patterns being similar to the reptiles and amphibians, i.e., distinctive eastern elements in northeastern Greece (e.g., marbled polecat *Vormela peregusna* and Eurasian ground squirrel *Spermophilus citellus*) and the Eastern Aegean islands (e.g., some Asian bats, a squirrel, and certain rodents). In contrast, the mountains that run southward toward Greece assist in hosting many "temperate forest species" that are restricted to the cool forest habitats and not found in the central lowlands or the south of Greece. As birds, migrating mammals probably played a role as aquatic biota dispersers for short distances, especially in the distant past.

6 Charting Biogeographic Ecoregional Boundaries Using Indicator Species

The object of our biogeographic review here is to describe regional-scale patterns of aquatic/semiaquatic species distributions along with conditions that help chart discernible "freshwater ecoregional units." We do this from the perspective of the territory of Greece but necessarily must look further beyond the political boundaries to appreciate the "ecosystem region" patterns over wider areas. This work is largely based on an aquatic fish faunal survey of river basins [31], and as in the FEOW [9], the freshwater fish taxa are used as primarily biogeographic indicators.

6.1 Complexity and Uncertainty with Biogeographic Indicators: Freshwater Fish in a Mixed-Method Approach

Since it is well known that freshwater fish distributions often largely reflect historical patterns of river basin drainage connections, fish-based biogeographic investigations continue to develop in Greece and the surrounding countries. Important distributional and phylogeographic reviews have already been completed for most freshwater fish species in Greece (e.g., [58, 98]); some detailed molecular genetic approaches are also investigating fishes at the populations' level. No other wholly aquatic group of organisms is so well studied in the wider study area. Despite progress, there is still a need for taxonomic investigations and detailed distributional studies since many taxonomic revisions are taking place. Genetic-level screening of populations is also important in exploring relations among species that may have been translocated by humans. Fish must be used with care in biogeographic investigations.

The issue of scale is paramount in developing fish-based biogeographic interpretations. At the ecoregion scale, we are initially interested in interpreting the broad patterns, a continental-scale biogeography [2]. It is therefore permissible to initially compile information from so-called parent river basins (i.e., the largest hydrographic basin units), ignoring the many small basins that have the imprints of local or subregion ecological and idiosyncratic historic effects on the fauna (e.g., extinctions from stochastic events such as epic droughts, human-induced extirpations, etc.). Figure 8 outlines the biotically based inventory procedure for compiling each major river basin's fish assemblage (presence/absence data) for delineating freshwater biogeographic regions; Greece's 23 major "parent" river basins are mapped. Figure 9 shows typical cluster analysis classification of the species to assess the "parent" river basin similarities. The major faunal breaks are defined using the "parent" river basins [7, 36]. Figure 10 produces a different cluster dendrogram when 105 river basins are used in the classification analysis [37]. Despite differences in species sets used, the major biogeographic boundaries are retained. However, the latter cluster analysis does create unexpected patterns due to confounding effects such as a small number of variant basins. For example, the Thrace ecoregion is awkwardly clumped near the Southeastern Adriatic since only two basins from the latter are included (Prespa and Aoos) (Fig. 10). Arbitrary cutoffs in such classification analyses should by no means be used as a sole guide to chart biogeographic regionalizations. Finer-scale approaches and the use of other evidence to discern biotic distinctiveness should be applied.

Mixed-method approaches (integrating quantitative and qualitative information) based on various assumption-free numerical analyses and through building a broader evidence-based biogeographic understanding must help guide final boundary decisions. Investigating site-based samples of species abundance, instead of presence/absence data, may also be very informative [39]. Whatever the numerical analyses used in exploring interbasin faunal relationships, uncertainties and data gaps will be better interpreted through a mixed-method approach. Both quantitative analyses and expert judgment have guided the original FEOW [9] delineations and earlier works at the ecoregional scale [2].

7 The Current Regionalization Framework: A Review of the Freshwater Ecoregions of Greece

Here we provide an updated freshwater ecoregion map of Greece (Fig. 11) and a brief review of each ecoregion. This work is based on the FEOW [9] baseline and reviews of freshwater fish and aquatic and semiaquatic species distributions. This is

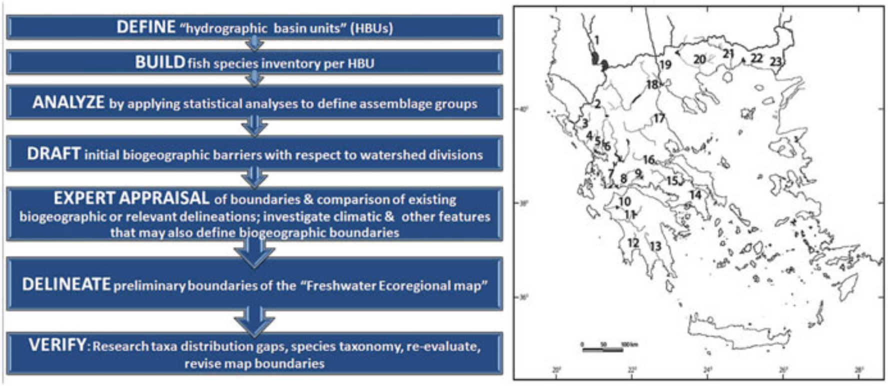

Fig. 8 Mixed-method procedure used to procure data, analyses, and delineations (*left*) and "parent" river basins which are larger than 700 km^2 and were used in initial analyses of fish-based classification and ordination: 1. Prespa, 2. Aoos, 3. Kalamas, 4. Acheron, 5. Louros, 6. Arachthos, 7. Acheloos, 8. Evinos, 9. Mornos, 10. Pinios (Peloponnese), 11. Alpheios, 12. Pamissos, 13. Evrotas, 14. Assopos, 15. Kifissos (Boeotian Kifissos-Kopais basin), 16. Spercheios, 17. Pinios (Thessalian Pinios), 18. Aliakmon, 19. Axios, 20. Strymon, 21. Nestos, 22. Filiouris, 23. Evros (adapted from [7])

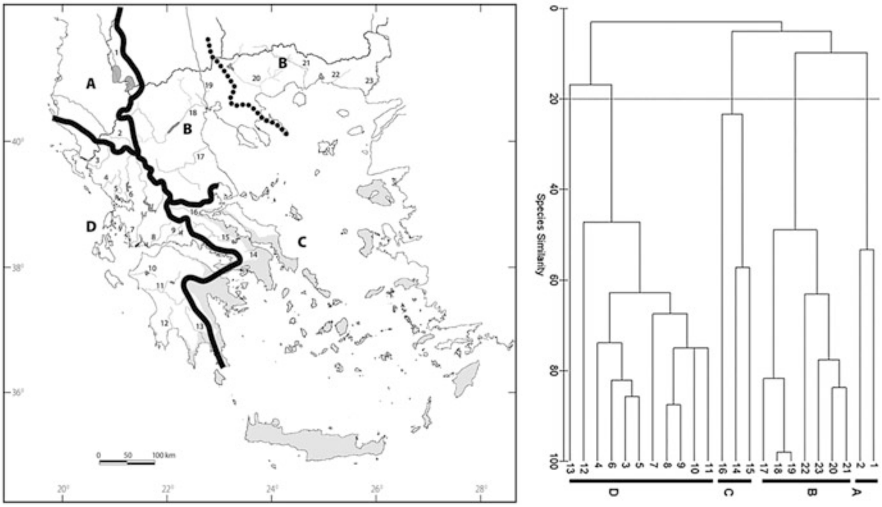

Fig. 9 An example of classification analysis of the major river basins based solely on fish species presence/absence (a subset of 90 lotic species). Cluster analysis (hierarchical clustering using group-average clustering from Bray–Curtis similarities) revealed four main biotically similar groups of basins at an arbitrary resemblance of 20%. This defines important faunal breaks on the watershed boundaries (*bold black lines*) of Greece's mainland. In this analysis lesser distinction is shown in the supra-region of the "Northern Aegean," area B split only by a *dotted line* (adapted from [7])

supplemented by knowledge of geological and climatological characteristics. We outline justifications for redefining boundaries and any changes made with respect to the FEOW [9]. Comparison among five important regionalization schemes is shown in Table 1, which tabulates the disparate biogeographic unit nomenclature as well. Efforts must be made to standardize the ecoregional/biogeographic regional names. We prefer to use the well-known anglicized names, instead of the local language-specific names in this review (i.e., Macedonia not Makedonia), but this has not held sway in earlier publications [14, 58].

7.1 Thrace

This is a species-rich region for aquatic biota; the so-called Thracian land bridge is located at the heart of the pivotal crossroads between the Balkans, Asia Minor, and the Black Sea Region. Freshwater biota has enriched the region due to a former connection with Black Sea and Danubian faunas (e.g., see [51]). It is an area rich in fish species, with at least 57 native species in the freshwaters of its Greek section [58]; large parts of this ecoregion expand into Turkey and Bulgaria. The Greek part hosts intriguing and specialized taxa such as lake-isolated shad species (*Alosa vistonica*, *Alosa macedonica*), migratory shemayas (*Alburnus volviticus*, *Alburnus vistonicus*), range-restricted loaches (*Cobitis puncticulata*), and Black Sea river gobies

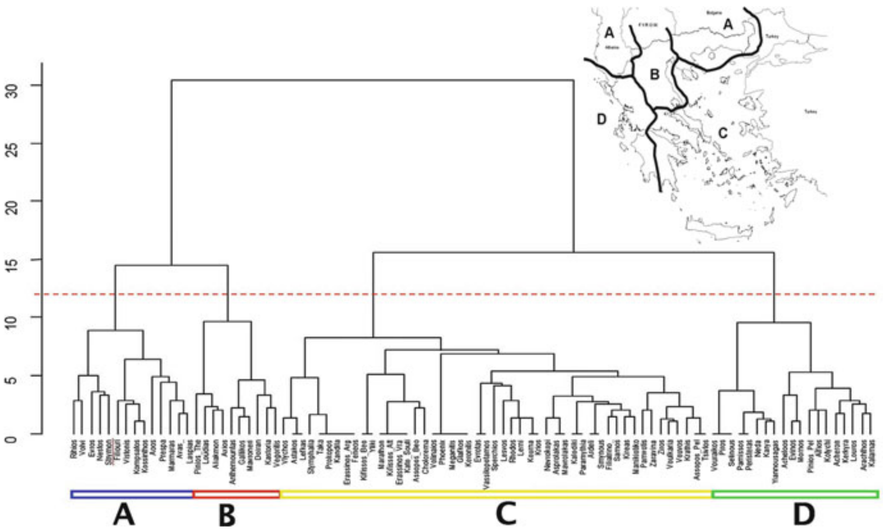

Fig. 10 Cluster analysis (Ward's method) with the presence/absence of all primary and primary-like freshwater fishes (120 native species) in 105 hydrographic basins. The arbitrarily defined cut-off at 12% creates four groupings: (**a**) "Thrace and Southeastern Adriatic", (**b**) Macedonia-Thessaly, (**c**) "Western Aegean and other islands," and (**d**) Ionian. The breakpoints between these groups are approximately projected on the *inset map* (adapted from [37])

(*Proterorhinus semilunaris*, *Neogobius fluviatilis*). Many of these species are related to species that are from the Danubian and Black Sea Region or are distributed further east in Asia Minor. Many fish genera are shared with the Macedonia-Thessaly region which also hosts Danubian species. Many other species of freshwater biota, including a freshwater shrimp (*Atyaephyra strymonensis*) and even a riparian willow (*Salix xanthicola*), are known to be restricted to the European part of this ecoregion. This richness is mirrored in terrestrial and semiterrestrial animals and many plants as well, which include terrestrial species from the Anatolian terrestrial fauna and flora as well, including some rare species restricted to this area within Greece [28, 122].

In Greece, the western limit of the ecoregion is a line of geologically old and stable mountains forming the watershed roughly between the Strymon and Axios river basin systems. The western boundary is enhanced by two idiosyncratic realms on this region's barrier line: the ancient lakes of the Mygdonia basin (Lake Koronia and Lake Volvi) and the rain shadow area and varied coasts of the Chalkidiki peninsula. The Mygdonia basin is a long-lived lake basin which functions as a refuge for various species from the Thracian ecoregion, while the Chalkidiki is a species-depauperate peninsula surrounded by deepwater areas creating a definite barrier to east-west freshwater species dispersal. The Chalkidiki peninsula is also a definite barrier for species dispersal between the Thrace and Macedonia-Thessaly Ecoregions

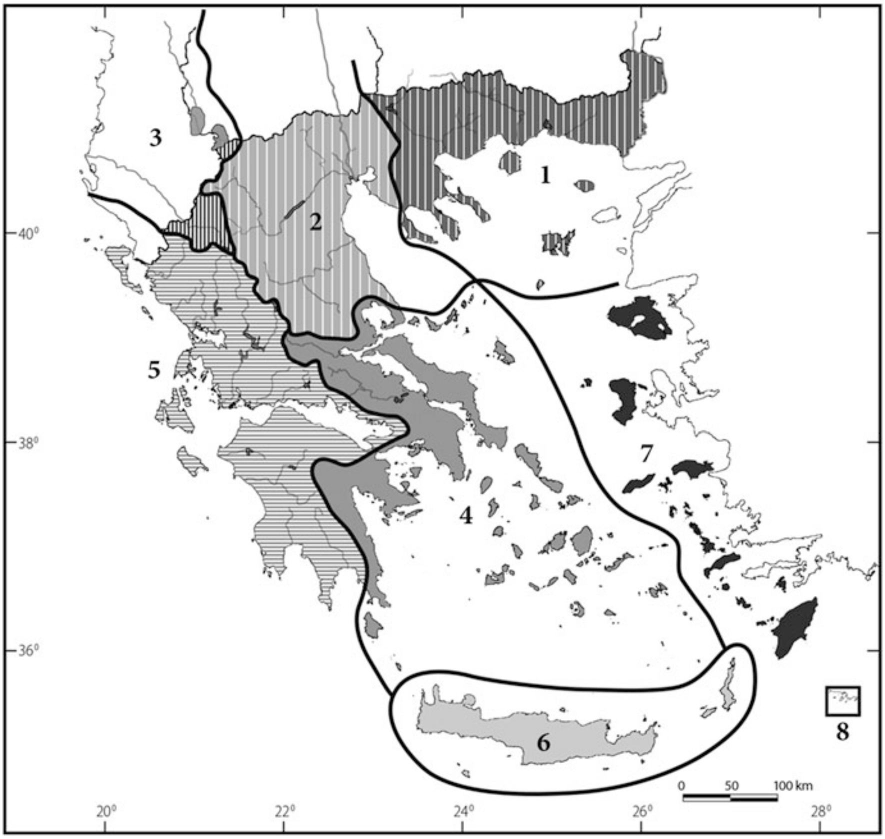

Fig. 11 Ecoregions of Greece, boundaries follow Zogaris [7] and the present study. Ecoregions *numbered* as in Table 1. See Fig. 2 for differences from the FEOW [9] of the study area

due to the deepwater marine areas around the peninsula (i.e., no significant confluences among major rivers where possible here during the Pleistocene sea-level transgressions) [123]. Despite this definite boundary area, in some fish-based biogeographic work, both Thrace and Macedonia-Thessaly have been charted together [124]; this supra-ecoregion has been called the "Northern Aegean."

There are still some poorly defined boundaries encompassing this region, especially outside the Greek territory. Bănărescu [14] charts the Thrace ecoregion exclusively in Europe, while Abell et al. [8] delineate it straddling both European and Asiatic shores of the Marmara Sea (Fig. 2). Since, during the last glacials, Thrace was fully connected with the northwestern basins of Asia Minor, the boundary of Abell et al. [8] should be justified; however, evidence for the specific boundary outline in Asiatic Turkey is required [125]. Finally the inclusion of the Northern Aegean islands of Limnos and Aghios Efstratios in this ecoregion should be better explored since they lie south of the North Aegean Trough which created a definitive deepwater

Table 1 The present study redefines some boundaries proposed initially FEOW [9] and reviewed in Zogaris [7]

	Present study	FEOW [9]	Bănărescu [14]	Maurakis et al. [15] (with subdivisions)	WFD 2000/60 ecoregions [4]
1	Thrace	Thrace	Thraki	Ponto-Aegean: Thracian-East Macedonian	Eastern Balkans (7)
2	Macedonia-Thessaly	Vardar	Macedonia-Thessaly	Ponto-Aegean: Macedonia-Thessaly	Eastern Balkans and Western Hellenic Balkans (7 and 6)
3	Southeastern Adriatic	Southeastern Adriatic drainages	South Adriatic-Ionian	Paleo-Hellas: Adriatic	Western Hellenic Balkans (6)
4	Western Aegean	Aegean drainages	Attika-Beotia	Paleo-Hellas: Attika-Beotia	Western Hellenic Balkans (6)
5	Ionian	Ionian drainages	South Adriatic-Ionian	Paleo-Hellas: Ionian	Western Hellenic Balkans (6)
6	Crete	Undefined region	Undefined region	Undefined region	Western Hellenic Balkans (6)
7	Eastern Aegean	Western Anatolia	Undefined region	Undefined region	Eastern Balkans (7)
8	Southern Anatolia	Southern Anatolia	Undefined region	Undefined region	Eastern Balkans (7)

The table compares nomenclature with four other ecoregion maps covering the study area. Some schemes had undefined areas, and these undesignated entities are mentioned. See Fig. 11 for delineations of the present study

zone separating the "European" continental shelf islands with the latter islands, which are geographically closer to the continental shelf area of the Troad of Asia Minor. Moreover, immediately to the south of the Troad, lies Lesbos, in the Eastern Aegean Ecoregion. Evidence-based guidance is needed to validate the proper ecoregional boundary around these islands since although the current boundary agrees with the phytogeography [17], others place a biogeographic boundary on the mid-Aegean Trough, i.e., between Samothraki and Limnos [22].

7.2 Macedonia-Thessaly

This diverse region is biologically closest to Thrace but with several important distinctive aspects and some different Danubian elements as well [33]. Its river basins include areas rich in wetlands and varied lentic surface waters, including several important ancient lakes, such as the Vegoritis basin lakes, Lake Kastoria and Lake Doirani. The last lake hosts at least one valid endemic fish species, and the former lakes have genetically distinct populations of fishes and invertebrate taxa. Like Thrace, Macedonia-Thessaly is also a fish species-rich area, hosting at least 49 native species in its freshwaters [58]. This rather small ecoregion hosts several range-restricted endemics, more than the Greek part of the Thrace ecoregion. This is due to the existence of more and older ancient lakes and to the unique geological history of the Thessalian Pinios basin as well [14]. The Pinios lowlands were a former lake bed, and it hosts three local endemic fish species (*Cobitis stephanidisi*, *Knipowitschia thessalus*, *Gobio feraeensis*) and several other genetically distinct fish taxa (i.e., local variant of *Barbus macedonicus*, etc. [58]). Paleogeographic research in the Thermaicos Gulf has shown that despite these distinctions, the Pinios was a tributary of the greater Axios paleo-river about 24,000 years ago [126].

As explained in Sect. 7.1 “Thrace,” Thrace and Macedonia-Thessaly have been shown to be ichthyogeographically closely related in numerical taxonomic classifications [124]. When solely considering riverine fishes, a relatively modest ichthyogeographic difference is detected between the Axios (Macedonia-Thessaly) and Strymon (Thrace) [36](Fig. 9). However, this close relation requires further investigation. If one adheres to the FEOW delineation of Thrace, which includes territory in NW Asia Minor, the ichthyological distinctions will carry more weight (i.e., if more river basins are included in the analysis). Nearly all holistic biogeographic publications support the ecoregional boundary between Macedonia-Thessaly and Thrace [7, 8, 14, 37, 39]. A frequently stated biogeographic hypothesis for such a different assemblage in Macedonia-Thessaly is that the Axios valley functioned as a dispersal “roadway” leading south for Danubian Morava-origin rheophilic fish and invertebrate species [14], and this is a key distinction between this ecoregion and Thrace for its fish fauna [31]. The relationship and possible biotic connections between the Axios and Danubian Morava may be explained by possible episodes of “river capture” (river piracy) since the headwaters of these rivers are in close proximity within Southern Serbia. Recent reviews show that new fish species splits are eminent in the Macedonia-Thessaly region, and new interpretations of the ichthyofaunal provenance of some species should prove the area as being even more ichthyologically distinct in the near future (see [58, 98]). This complex fish-based boundary controversy shows the importance of providing mixed-method evidence for delineations in precautionary incremental steps.

Finally the name Macedonia-Thessaly was proposed by Maurakis et al. [15] and Bănărescu [14], and we use this instead of “Vardar” as proposed in FEOW [9]. Vardar is a Slavic name for a single river (Axios/Vardar) in this otherwise very diverse and culturally prominent region; we feel it is proper to use the classical geographical names that best help distinguish the region.

7.3 Southeastern Adriatic

Although most of the region lies within Albania, parts of the Aoos and Prespa Lake tributary basins are in Greek territory. This ecoregion is one of the most endemic species-rich; however, its aquatic species taxonomy, phylogeography, and general biogeography are poorly studied. This ecoregion holds a long-isolated fish species assemblage and one that has evolved and diverged due to important vicariance events and the existence of long-lived lakes (Ohrid, Prespa, and Skadar) [14]. The region is rich in fish species [127]; about 20 native freshwater species are recorded in the part of these basins that belong to Greece [58]. There are only very few affinities with the Thrace and Macedonia-Thessaly regions (i.e., some Danubian genera that have since diverged [98, 103]). This region has remarkable differences with the adjacent Ionian region to the south; however it has many "shared species absences" with the Ionian since relatively few Danubian fish species exist in both the Southeastern Adriatic and Ionian. The region also has a higher percentage of regionally endemic fishes than Macedonia-Thessaly or Thrace.

The southern boundaries of this region are fairly distinctive. A rather abrupt faunal break exists in the southern rim of the Aoos basin watershed divide, i.e., between the Aoos and Butrint/Kalamas basins. The Butrint basin includes the Bistrica river, located just north of the Greek-Albanian border but belonging to the Ionian ecoregion. This boundary was originally charted by Bianco [128], but it was not identified in a later descriptive analysis [33]. Bănărescu [14] showed this boundary on a map, but in his detailed description, he defined a broader regional unit, the "Ionian-South Adriatic," as a single biogeographic region. Zogaris et al. [36, 37], Oikonomou et al. [124], and Economou et al. [39] confirm the Butrint/Kalamas-Aoos boundary (although it was erroneously charted in the FEOW (2009) map (Fig. 2)).

The coastal marine depths between the Aoos and Butrint basin help define the southern boundary. The steep sloping continental shelf along the southern Albanian coast (Strait of Otranto) effectively separates the Butrint from the Aoos basin, presumably even during sea-level regressions which took place during the Tertiary and Quaternary [123]. It is possible that the Southeastern Adriatic biogeographic unit has been influenced by incursions of species from the Danube due to river piracy among the Danubian Sava and Drin tributaries. This makes it distinctly different from the Northern Adriatic also [124].

Finally the ancient lakes of Ohrid and Prespa represent a world-renowned endemicity hotpot, and they are biogeographically related to the faunas of the north and south of Albania, respectively [127]. Phylogeographic relationships of several freshwater fishes of Prespa with the southern Albanian drainages (formerly endemics of Prespa) have been recently clarified [129]. The unresolved taxonomic status of several fishes in the area and poor knowledge of their distribution have created difficulty in charting biogeographic boundaries. We therefore propose one should not consider the Prespa lake basin (or a wider entity including Ohrid) as a distinct biogeographic region as has been published by Oikonomou et al. [124]. Ohrid has a higher overall endemicity than its shallower sister Lake Prespa, and their faunas are remarkably different [130]. Both lakes as is Lake Malik are hydrologically connected to the Adriatic. Finally the Prespa basin area, which has an areal cover of about 2,520 km^2, does not constitute a large enough areal entity to be considered an "ecoregion" (as compared to other biogeographic regional units or the freshwater ecoregion areas [9]). Nevertheless, Lake Prespa and Lake Ohrid are globally important biodiversity hotspots and should be considered distinct parts of the Southeastern Adriatic freshwater ecoregion.

7.4 Western Aegean

This is a rather small freshwater ecoregion and the most geographically fragmented such entity in Greece. For a long time, the eastern coast of mainland central Greece south of and including the Spercheios basin was called the Attiko-Beotian region [15, 131]. The FEOW [9] expands this region; it now includes the Western Aegean islands (Cyclades, Euboea, Northern Sporades) and the northeastern parts of the Peloponnese peninsula. Zogaris [7] corroborated the general regionalization but modified these boundaries to follow watershed lines belonging exclusively to the Aegean basin, as presented in Fig. 11. This ecoregion includes an extensive rain shadow area that sustains a seasonally semiarid area with frequent prolonged droughts (this is a climatically homogenizing effect created by the Pindus cordillera). Most of the area is made up of dry-land calcareous mountainous landscapes with rather scarce running water ecosystems and many small-sized seasonally arid river basins. Although the area's "small waters" (i.e., springs, rivulets, etc.) host many interesting local endemics – especially of smaller aquatic animals such as spring-inhabiting aquatic snails [75–77]– the region is generally considered species-poor for aquatic life. Although this is so for fishes and many larger aquatic plants due to the scarcity of larger permanent waters, its aquatic invertebrates are poorly studied and may include many undescribed taxa [76, 91].

This is a difficult ecoregion to delineate. Some boundaries are still poorly justified in a biological sense [7]. The region hosts about 30 native fish species in its waters and most are actually widespread marine migrants and transients; some species need further taxonomic research, including the *Alburnoides* and *Rutilus* of the Spercheios, *Squalius* of Euboea, *Aphanius*, and *Knipowitschia* [58]. This geographically fragmented complex of peninsulas and islands hosts only three major "parent" river basins holding substantial fish faunas (i.e., Spercheios, Kifissos-Kopais, and Assopos). The region sustains very few lakes, one of them a marshy extensive ancient lake area, the greater Kopais basin (including the Kifissos and Lake Yliki and Lake Paralimni) in Boeotia. This is the region's most endemic-rich area with emblematic fishes such as *Telestes beoticus*, *Scardinius graecus*, and *Rutilus ylikiensis*, while the enigmatic *Luciobarbus graecus* is shared with the Spercheios. Further north, the river Spercheios is exceptional since it is a biogeographic crossroads also hosting several fish genera from the Macedonia-Thessaly freshwater ecoregion [39]. Fish phylogeography also provides evidence for a connection between the Spercheios and the Pagasitikos Gulf to the north (the Pelion peninsula being a biogeographic barrier).

Ecoregional boundary justification becomes difficult especially in the southern part of this region. The remarkably dry limestone landscapes of the eastern Peloponnese, the Saronic and Argolic Gulfs and the Cycladic islands, have very few stretches of perennial streams or other permanent water; this is one of the driest parts of the country. The eastern Peloponnese is also a rain shadow area with many "shared species absences" with the Attiko-Beotian heartland. In this way the eastern Peloponnese is similar to the other Western Aegean drainages, but the boundary lines are difficult to set precisely. Taxa-particular distributional idiosyncrasies complicate boundary issues, since in some parts of this region, as in the Ionian ecoregion, many spring-inhabiting endemics thrive [95]. Many zoologists have considered the Peloponnese a distinct biogeographic unit (see [7]), although some who study aquatic biota have also provided evidence for an east-west split (e.g., [26]). The east-west boundary within the Peloponnese, as prescribed in this study, requires further research.

This region includes the Cyclades islands which during the Pleistocene glaciations were much larger “mother-island” entities surrounded by smaller islands. The Cyclades were also probably connected via Attika and Euboea, during the middle Pleistocene, ca. 180–140 kya BP [132]. Despite their current aridity, the Cyclades surprisingly host several endemic aquatic insects [91, 133] and many terrestrial invertebrates as well [134]. Euboea is Greece’s second largest island, a true continental island that was connected to Boeotia and Attica during the early Holocene, a few thousand years ago. However, Euboea’s long and rather high mountains are geographically and geologically isolated, creating river basins that are long independent from the mainland’s basins. This long mountainous island is unusual in being relatively rich in significant spring-fed perennial flowing streams that also host endemic macroinvertebrates [75] and even two endemic fish taxa, an undescribed chub *Squalius* sp. and the critically endangered Evia barbel *Barbus euboicus* [58].

Since the Western Aegean’s aquatic animals are still rather poorly inventoried [14, 84, 91] and perennial surface water features are patchy and isolated, the particular biogeographic boundaries have never really been precisely charted. The delineation of the “Aegean drainages” freshwater ecoregion by FEOW [9] is unfortunately inaccurately and coarsely charted since it erroneously includes basin areas that have no biogeographic relationship to this particular region (i.e., the northern Corinthian Gulf drainages which obviously drain into the Ionian basin and parts of Thessalian Northern-Pelion and Mavrovouni mountains which have relations with the fauna of northern Greece) (see Fig. 2). Therefore, this ecoregion’s final delineation is obviously in need of documented evidence in order to verify the redefined boundaries in our revised map (Fig. 11).

7.5 Ionian

Greece’s west coast surface waters are collectively the most endemic species-rich freshwater ecosystems in the country. A small part of this ecoregion also belongs to the southernmost part of Albania (the Butrint basin and Bistrica river, south of the Aoos watershed). Many endemic fish and other aquatic animals are extremely range restricted in this, or in isolated parts of this, ecoregion [31]. The region has about 48 native fish species in its freshwaters [58]; however, basin-scale species richness is much poorer than Macedonia-Thessaly or Thrace [39]. In mainland Greece native fish distributional patterns clearly indicate that the Pindus mountains create a prominent long-term biogeographic discontinuity that separates distinct freshwater biogeographic regions east and west of the Pindus, something well depicted in many biogeographic studies of the wider region [33, 124]. The Pindus biogeographic barrier has been corroborated by the distributions of many animals and plants including selected amphibians [107]; semiaquatic terrapin; *Emys orbicularis*, among other species [135]; floristic assemblages [60]; and selected aquatic invertebrates, such as the Hydrobiidea gastropods [14] and freshwater shrimp [85]. Despite its remarkable isolation by the ribbonlike Pindus mountain chain, there is much variation within this ecoregion.

One of the most outstanding aspects that characterize this ecoregion is the remarkable diversity at the subregional level. Parts of the region have unique water bodies, isolated in the past by former inland lakes, such as the Corinthian Gulf, or long-standing fairly large river basins with extant long-lived lakes, such as the Acheloos. The lotic waters around the ancient lake of Trichonis are especially interesting [136], and new species are still being described in this global biodiversity hotspot. Distinctive and long-isolated basins such as the Evrotas, for example, are unique and idiosyncratic for their range-restricted endemics and depauperate biocommunities, well adapted to non-perennial and spring-fed stream conditions [57]. Of the river basins included in this heterogeneous ecoregion, the so-called northern Ionian (northwest of the Acheloos watershed line) seems to create a distinctive subregional entity. Many species of fish are restricted to this area, including distinct species of the genera of *Pelasgus*, *Squalius*, *Telestes*, *Knipowitschia*, *Valencia*, and *Cobitis*. Work on aquatic invertebrates in the Ionian ecoregion will reveal very interesting biogeographic interpretations, including new species and informative subregional patterns; a productive area is research on freshwater mussels [137], freshwater shrimps [85, 138], and fish parasites [59]. More research into the fishes and other aquatic life of the Ionian ecoregion is required, and new species will certainly be described in this relatively understudied "center of endemism."

All the offshore Ionian Islands are definitely a part of the Ionian ecoregion, and they constitute a species-depauperate area compared to the varied biotic riches of the adjacent mainland. An exception to this is Kerkira, which is really a recently isolated continental island, being connected to the mainland 8,000 years ago [50]. The island waters were obviously connected to the Kalamas and Butrint basin, and today the island still sustains diverse stream and wetland ecosystems [104, 139]. As would be expected, the Ionian Islands' aquatic fauna is very similar to the mainland. For example, the Ionian Islands share a similar caddisfly fauna (Trichoptera) with the mainland's west coast, in contrast to the many endemics found in the Aegean islands [81]. Similarly, the flora of the islands also has more connections to the mainland than in the endemic-rich Aegean [140]. Even some species of isolated fish are genetically closely related to the west coast mainland species [141], and there are no endemic fish species known to be restricted to any of the islands [104].

7.6 Crete

Crete has been called a small "continent" due to its distinctiveness and diversity [142]. Van der Geer et al. [114] refers to Crete as an "oceanic-like island" for its unique geological and zoogeographical history. This proposed freshwater ecoregional unit includes Crete and its satellite islets and the Karpathos archipelago (with three main high-relief islands and about 20 very small islets). Controversy about the biogeographic ecoregional status of Crete and its surrounding islands persists.

Phytogeographically, Crete is a separate floristic region, noted as "Kriti + Karpathos" in the Flora Hellenica map [17, 60]. With respect to the Karpathos archipelago cluster, Raus [143] concluded that botanic relations are to the west, to the "European" Cretan and south Aegean flora, rather than to the Asian flora of the other Dodecanese Islands. The Karpathos archipelago has several faunal elements not found in Crete but exhibits many "shared species absences" relative to the species-rich Dodecanese, which are nearer to the Asian coast. However, nearly all zoologists traditionally group the Karpathos islands toward the Asian Dodecanese and not with Crete. The Karpathos archipelago has been geologically isolated from the Cretan landmass for over 10 MYA; however, inclusion within a broader Crete ecoregion is justified based on the internal endemism seen among the different former "paleo-island" sectors of Crete. In this way the Crete Freshwater Ecoregion can be conceptualized as an "insular" ecoregion linking isolated but geographically proximate and geologically similar areas together. The FEOW [9] global freshwater ecoregion delineation did not classify the Cretan area to a particular ecoregion; Crete along with Karpathos-Saria-Kassos was labeled as "undesignated" on the global FEOW map. During the development of the expert-guided process of the FEOW project, there were differing opinions about the place given to the island, and one of the early maps had erroneously lumped the island to Southern Anatolia and Cyprus (Abell, R. pers. com). In contrast, Crete is a distinct ecoregion in the terrestrial ecoregions of the world map but without the Karpathos archipelago [11, 45] (Fig. 5). Crete was proposed as an independent freshwater ecoregion in Zogaris [7], and in this account we suggest a distinct freshwater ecoregional status for Crete and the Karpathos archipelago.

The wider geological context here is important for interpreting the proposed ecoregion's boundaries and its relationship and affiliation to other geographic areas [114, 144–146]. For nearly six million years, Crete have been completely isolated from the continent. About 15 MYA Crete belonged to a large subcontinent that extended from the Western Balkans to Asia Minor. The Aegean landmass subsided under the sea beginning 10 MYA, and only the higher mountains, the so-called Cretan paleo-islands, remained above water. This period of vicariance within the island chain augmented evolutionary development in many species [62, 83]. The Karpathos archipelago was also isolated from Asia, long before Rhodes, and it has been isolated from Rhodes for at least 3.5 MYA [145]. Around 2 MYA, the wider region of Crete was tectonically uplifted and much land emerged, and the palao-islands were joined to form Crete's present-day outline. Crete is characterized by an impressive and ancient mountain range system with four steep massifs and more than 20 satellite mountains. Karpathos, Saria, and Kassos although very narrow and steep islands also have very high mountain ridgelines and gorges similar to Crete.

Climatic conditions and hydrology also connect Crete and the Karpathos archipelago. The eastern part of Crete and the Karpathos archipelago are located within a prominent rainshadow (created by the Cretan mountains), and this produces some of the driest conditions in Europe in Eastern Crete [142]. Crete's running waters are diverse, but many are non-perennial flowing and subterranean; surface water ecosystems are stressed due to both high evapotranspiration rates, climatic variability, and widespread human-induced water over-abstraction [147]. Naturally arid ephemeral streams dominate in Eastern Crete and the Karpathos islands, and some are nearly like semidesert wadis. The eastern part of Crete and the Karpathos area are a very windy part of the Aegean compared to the more leeward relatively calm conditions on Rhodes [148]. In this way climatically and geologically, the Karpathos archipelago shows more affinity with Eastern Crete than the more humid conditions and gentle landscapes of Rhodes.

Since geologically isolated islands such as Crete are prone to natural and anthropogenic extinctions, these islands have very few native fish species. Crete is definitely one of the poorest ecoregions for native fish fauna in the Mediterranean as nearly all native fishes in inland streams and lakes are of marine origin (about 11 native species). Actually only a very few native species live all their life cycle in inland waters, namely, the localized river blenny *Salaria fluviatilis* and landlocked smelt *Atherina boyeri* [149]. For this reason, invertebrates, the fossil record, and perhaps water plants should be better explored for the region's freshwater biogeographic description. Although, endemism among the extant terrestrial plants and invertebrates is impressively high, most aquatic species distributions are not well studied [42]. Also, the aquatic biodiversity of Crete is probably characterized by the extirpation of several aquatic species due to modern anthropogenic wetland and surface water degradation [65, 142].

Today, Crete and the Karpathos archipelago certainly have a depauperate freshwater biota relative to the large continental islands or peninsulas of the Balkans and Asia Minor, but there is a relatively high number of endemic freshwater and wetland invertebrate life forms, including endemic aquatic insects (e.g., Trichoptera, Coleoptera, Heteroptera, Plecoptera, among other groups), freshwater crabs, a freshwater shrimp, and endemic amphibians. Because the Crete ecoregion is a long-isolated "former" island chain, its overall uniqueness is well known [146, 150], but further study of its aquatic and wetland species is definitely required for a complete biogeographic review. Finally a thorough evaluation of the freshwater biogeographic affinity among Crete and the Karpathos archipelago must be researched. For now, we take a precautionary approach and suggest union of the Karpathos archipelago with Crete.

7.7 Eastern Aegean

Most of the Greek islands in the Eastern Aegean show biological affinities to the faunal assemblages of Asia Minor, but freshwater assemblages are comparatively species depauperate to the adjacent Asian continent. Unfortunately, the aquatic biota remain poorly studied, and new species have been recently recorded and described in the area, such as on the wetland-rich Lesbos island [151]. The Eastern

Aegean islands have few freshwater fish; although at least 18 native species inhabit freshwaters, only six are confirmed primarily freshwater fishes. All native primary freshwater species show strong affinity to Asia Minor [58, 152]. Abell et al. [8] correctly regard the Eastern Aegean islands as part of their so-called Western Anatolia Freshwater Ecoregion (see Table 1); other researchers use the name "Eastern Aegean" to be consistent with marine area geographic terms often used in other regionalizations [35].

The literature provides full biogeographic support to the notion that these insular ecosystems should constitute part of an ecoregion that belongs to western Asia (Anatolia) [119, 153–155]. Botanists, such as Strid [17], call the biogeographic line at the mid-Aegean trench "Rechinger's line" which in his words "constitutes the phytogeographical borderline between Europe and Asia" in the Aegean. However, there are varied patterns in the aquatic biota distributions among the different islands. Some islands such as Tilos, Fournoi, Nissiros, and Kalymnos, for example, have very little surface water, and their freshwater biota is relatively unknown. Some islands were rather recently connected to the Asian mainland less than 10,000 years ago (Lesvos, Chios, Samos, Kos), while others, such as Rhodes, had separated approximately three million years ago [145].

Rhodes is especially interesting due to its long-term insular isolation, its southern location near the Southern Anatolian shores, and rather diverse stream ecosystems. Although the island has a unique endemic fish (*Ladigesocypris ghiggi*), it also sustains a species of freshwater shrimp (*Palaemon colossus*), which it shares with the Southern Anatolian Ecoregion [85]. Rhodes is also remarkably isolated from the southernmost of the Dodecanese Islands, Karpathos, and Kassos – totally separated perhaps for at least 3.5 MYA [24] – while these two islands are attributed by phytogeographers to the Crete ecoregion. Baseline species inventory work and research are urgently required on both Eastern Aegean islands and the adjacent Anatolian shores in order to explore freshwater biotic relations and provide for potential subregional delineations and a thorough biogeographic interpretation.

7.8 Southern Anatolia

Greece administers a tiny island cluster of just 11 rocky islets and sea rocks, the Kastellorizo cluster, along the Mediterranean coast of Southern Anatolia. This island cluster lies just 2 km off the Anatolian shore and lies east of the Western Aegean-South Anatolia division boundary as charted by Abell et al. [8] and other terrestrial and aquatic biogeographic delineations of Asia Minor (e.g., [125, 156]). The Kastellorizo island group has no large wetlands apart from tiny micro-springs and temporary pool-like depressions, sometimes flooded in the winter season; the stream courses are only ephemeral gullies, and there are a few artificial cisterns, wells, and a tiny modern reservoir [157]. The tiny artificial water bodies hold a very few hydrophilous plants [158]. Of course, no native freshwater fishes exist on the island. It does host a terrestrial amphibian, that is definitely a species of Southern Anatolia, the

Lycian salamander (*Lyciasalamandra luschani*) (Fig. 7), but we have no knowledge of its hydrophilous invertebrate fauna in its few aquatic/semiaquatic ecosystems. The biogeographic boundaries of Southern Anatolia are not well explored [125]. Research is needed to confirm the Eastern Aegean/Southern Anatolian ecoregional boundary and to better define the latter.

8 Discussion

8.1 Freshwater Ecoregions as a First-Tier Biogeographic Framework

The current freshwater ecoregional map of Greece provides a holistic regionalization framework, grouping river basins based on major biotic similarities and relevant geological and climatic attributes. As Bailey [1] has said: "such exercises in regionalization approach truth by a series of approximations." Despite this current map's mixed-method approach and expert-guided procedure with the associated caveats [7], the ecoregional units have already been very useful in inventory and conservation research (e.g., [39, 58, 159]). The freshwater ecoregion map is suited for in-depth, intraregional analysis that could better support boundary validation and the definition of biogeographic "subregions" in order to further assist river basin classification [160]. Finally, we reiterate Forman's [161] wise words: "Regional ecology is a little-understood research frontier that will noticeably strengthen conservation, planning, sustainability, and land-use policy. We had better learn the ecology of regions."

8.2 Taxonomic Complexities and the Taxonomic Impediment

Freshwater fish distributions have traditionally guided aquatic biogeography. One current problem with solely using fish in regionalizations is taxonomic. An unprecedented percentage of European fish species name changes has taken place in the last two decades [127]. Most of the changes have resulted from the application of new taxonomic concepts and methods, especially the adoption of the phylogenetic species concept (PSC), which has now replaced the biological species concept (BSC) (for a review, see [31]). Traditionally, under the BSC, a "species unit" is a group of actually or potentially interbreeding populations. The PSC, by contrast, considers "species" as the smallest diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent. In this context, the PSC accepts the evolutionary potential of a lineage that has just started to separate from other lineages as the main criterion for defining species. Thus, under the PSC, there are no subspecies. As a result, many taxa recognized as subspecies under the BSC have often been raised to the species rank. As taxonomic research continues, former species and subspecies will either tend to be "split" into distinct species or "lumped" within already valid species [141]. Several new freshwater fish species are expected to soon arise through this research within the area of Greece's territory [58]. Ongoing research in the fish populations' systematics and phylogeography will continue to guide constituent freshwater biogeographic boundaries.

These taxonomic complexities obviously spread to all species, not just fish. If current species distributions are to be utilized in biogeographic analyses, adequate taxonomic and phylogeographic information must be inventoried, organized, interpreted, and published. Part of the reasons for very different approaches to freshwater biogeographic delineations is that Southeastern Europe's species-level taxonomy is still far from being resolved, and there are still data gaps in basic biodiversity distributional knowledge [41]. There is no better time to restate the value of organizing a broadscale effort for a full biodiversity inventory of inland waters. We believe foreign and Greek professional researchers and amateur naturalists should coordinate and participate in collections in Greece. The "taxonomic impediment," reflecting a global shortage of taxonomists and systematists which negatively impacts biodiversity conservation, is a worldwide problem [162]. Organized biological collection campaigns, taxonomy, and phylogeography should become defining priorities for conservation-relevant aquatic research in Greece and other Mediterranean countries [163].

Finally, a rising issue in biogeography is xenobiodiversity, the increase and spread in non-indigenous species that are artificially dispersed by humans. Here too, due to the taxonomic impediment, this issue has been poorly monitored in inland waters in Greece [164]. This concerns both alien species from abroad and locally translocated species from nearby ecoregions. In some cases, it is difficult to be sure if certain populations are translocated or have a naturally disjunct distribution. An example is the unusual Caucasian goby (*Knipowitschia caucasica*) population in a coastal stream near Karystos on Euboea Island; its genetically closest relatives are in the Thracian Ecoregion [165]. Since a genetic screening of other Western Aegean *Knipowitschia* gobies has never been done, we cannot be sure if the Karystos population is natural or introduced by humans. Evidence for species translocations across ecoregions, involving both vertebrates and invertebrates native to Greece – but not indigenous to the river basin areas they currently inhabit – is a serious conservation concern (e.g., [84, 159]). Monitoring for biodiversity must necessarily study xenobiodiversity to interpret patterns, trends, and impacts to local biodiversity.

8.3 Freshwater Ecoregion Delineation Difficulties

Hartshorne [166] described the concept of region as being characterized by "relative homogeneity in prescribed characteristics, selected for their salience in highlighting areal differences at the regional scale." In Greece, it has been repeatedly shown that freshwater fish assemblages can effectively depict dispersal barriers and the influence of hydrographic history and paleogeography [15, 34]. However, fish-based classification of river basin relatedness does have limitations in species-depauperate areas dominated by very small basins and islands [36]. These challenges are instrumental in terms of identifying basic needs for evolving better methods to delineate ecoregion boundaries [2, 44, 167].

Greece and the surrounding Eastern Mediterranean countries are also challenging areas for tracing biogeographic patterns at the regional scale because of the intensive influence humans have had on ecosystem modification and cultural landscape patterns [116]. In zoogeographic and vegetational sense, this has been most intensive in the southern half of Greece and the islands [116, 168]. Species-depauperate conditions in some areas of the south may point to recent anthropogenic extirpation instead of "natural" biogeographic patterns; a potential example of this is the species-poor riparian zones in more populated and degraded river basins of southern Greece [70]. Humans have also transported/translocated many species, especially on the islands (e.g., [116, 169]), in reservoirs, and in larger river basins [159]. Humans have shaped the landscape patterns in such a way as to sculpt the evolution of so-called cultural landscapes, where human-modified habitat types now dominate [168]. In the Greek islands, human influence has been widespread for at least 8,000 years [48, 142].

It should be made clear that on the islands and peninsulas, there are naturally increased extinction rates [108]. Detailed work to define exact ecoregional (and subecoregional) boundaries is needed in the islands and the southern half of Greece's mainland due to the natural (or human-induced) species-depauperate conditions. Macroinvertebrates are important target groups for biogeographic research here, and their communities may differ markedly from adjacent mainland conditions, e.g., the near-natural streams of Samothraki Island [170]. Many small streams in the islands may sustain macroinvertebrate communities that have survived totally isolated for millions of years [133], and many of these are still poorly explored [14, 42, 171]. Inventory and taxonomic work will provide scientific justification for the legislative conservation of the so-called small waters of the islands and xerothermic Mediterranean coasts; many of these areas' small streams and wetland conservation values have long been underappreciated [76, 163].

9 Conclusions

Ecoregional maps may inspire controversy, but they are also powerful organizational, educational, and exploratory tools. Charting biogeographically based freshwater ecoregional units has been especially challenging in Greece since tectonic, climatic, sea-level, and anthropogenic changes have created outstanding complexity. The eight freshwater ecoregion delineations that encompass Greece's territory are akin to the "Freshwater Ecoregions of the World" [9] delineations, but specific boundaries have been redefined in this review. We strongly suggest a revision of the FEOW [9] boundaries based on the incremental revisions in this study for Greece.

Although Greece is a living laboratory for biogeographic studies, many of the aquatic biota have been poorly studied. Extensive aquatic and semiaquatic species distributional inventories will be required for a full review and more complete interpretation of freshwater biogeographic patterns. Particular emphasis must be given to key indicator aquatic groups for inland waters, such as the EU WFD's biotic quality elements: fishes, benthic macroinvertebrates, and aquatic plants. This will help couple policy-relevant EU water management with biodiversity conservation initiatives. A detailed fish atlas (and associated archive of specimen and genetic collections) is an imperative for furthering any kind of organized fish-based biogeographic and phylogeographic work. Fish populations require genetic screening, and novel molecular analytical methods now help speed up the inventory process. Currently, data on the taxonomy and precise distributions of aquatic macroinvertebrates is particularly poorly developed in Greece, and these groups are highly important aquatic biogeographic indicators. Researchers from Greece and other countries must cooperate to increase the intensity of organized field collections. Biogeographical research should provide an impetus to coordinate more productive taxonomic and phylogeographic research that will ultimately assist scientifically guided conservation actions.

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References

1. Bailey RG (1998) Ecoregions: the ecosystem geography of the oceans and continents. Springer, New York, NY
2. Abell R, Thieme M, Dinerstein E, Olson D (2002) A sourcebook for conducting biological assessments and developing biodiversity visions for ecoregion conservation. Freshwater ecoregions, vol II. World Wildlife Fund, Washington DC
3. Turak E, Dudgeon D, Harrison IJ, Freyhof J, De Wever A, Revenga C, Garcia-Moreno J, Abell R, Culp JM, Lento J, Mora B (2017) Observations of inland water biodiversity: progress, needs and priorities. In: Walters M, Scholes RJ (eds) The GEO handbook on biodiversity observation networks. Springer, Cham, pp 165–186
4. European Commission (2000) Directive 2000/60/EC, Establishing a framework for community action in the field of water policy. Off J Eur Comm L 327:1–71. Brussels
5. Gordon ND, McMahon TA, Finlayson BL, Gipple CJ, Nathan RJ (2004) Stream hydrology: an introduction for ecologists 2nd edn. Wiley, Chichester
6. Montgomery DR, Buffington JM (1998) Channel processes, classification, and response. In: Naiman RJ, Bilby RE (eds) River ecology and management: lessons from the Pacific Coastal Ecoregion. Springer, New York, NY

7. Zogaris S (2009) Contribution to a biotic classification of the rivers of Greece based on ichthyofauna and riparian vegetation. Doctorate Degree in Environmental and Natural Resources Management, University of Ioannina, Agrinio. (in Greek)
8. Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N, Coad B, Mandrak N, Balderas SC, Bussing W, Stiassny ML (2008) Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. Bioscience 58(5):403–414
9. FEOW (2008) Freshwater ecoregions of the world-conservation science program. The Nature Conservancy and World Wildlife Fund, Washington DC
10. Bailey RG (2005) Identifying ecoregion boundaries. Environ Manag 34:14–26
11. Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on earth. Bioscience 51:933–938
12. Omernik JM (2004) Perspectives on the nature and definition of ecological regions. Environ Manag 34(1):S27–S38
13. Holt BG, Lessard JP, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, Fabre PH, Graham CH, Graves GR, Jønsson KA, Nogués-Bravo D (2013) An update of Wallace's zoogeographic regions of the world. Science 339(6115):74–78
14. Bănărescu PM (2004) Distribution pattern of the aquatic fauna of the Balkan Peninsula. In: Griffiths HI, Kryštufek B, Reed JM (eds) Balkan biodiversity: pattern and process in the European hotspot. Kluwer Academic Publishers, Dordrecht
15. Maurakis EG, Pritchard MK, Economidis PS (2000) Historical relationships of mainland river drainages in Greece. Bios 6:109–124
16. Lymberakis P, Poulakakis N (2010) Three continents claiming an archipelago: the evolution of Aegean's herpetofaunal diversity. Diversity 2:233–255
17. Strid A (1996) Phytogeographia Aegaea and the Flora Hellenica database. Ann Nat Hist Mus Wien Ser B Bot Zool:279–289
18. Rechinger KH (1943) Flora Aegaea. Flora der Inseln und Halbinseln des ägäischen Meeres. Akad Wiss Wien Math-Naturwiss Kl Denkschr 105(1)
19. Turrill WB (1929) The plant-life of the Balkan Peninsula: a phytogeographical study, vol 1. Clarendon Press, Oxford
20. Watson GE (1964) Ecology and evolution of passerine birds on the islands of the Aegean Sea. PhD. Thesis. Yale University, New Haven, CT
21. Giokas S (2000) Congruence and conflict in Albinaria (Gastropoda, Clausiliidae). A review of morphological and molecular phylogenetic approaches. Belg J Zool 130:93–100
22. Kougioumoutzis K, Valli AT, Georgopoulou E, Simaiakis SM, Triantis KA, Trigas P (2016) Network biogeography of a complex island system: the Aegean Archipelago revisited. J Biogeogr. doi:10.1111/jbi.12920
23. Poulakakis N, Kapli P, Lymberakis P, Trichas A, Vardinogiannis K, Sfendourakis S, Mylonas M (2014) A review of phylogeographic analyses of animal taxa from the Aegean and surrounding regions. J Zoolog Syst Evol Res 53:18–32
24. Sfenthourakis S, Triantis KA (2017) The Aegean archipelago: a natural laboratory of evolution, ecology and civilisations. J Biol Res Thessalon 24(1):1–13
25. Ganiatsas K (1967) Phytogeographia, Thessaloniki
26. Audiso P, De Biase A, Jäch MA (1996) Greek species of the genus Hydraena (subgenus Haenydra Rey) (Coleoptera, Hydraenidae). Aquat Insects 18(2):65–90
27. Dimopoulos P, Raus T, Bergmeier E, Constantinidis T, Iatrou G, Kokkini S, Strid A, Tzanoudakis D (2013) Vascular plants of Greece: an annotated checklist. Botanischer Garten und Botanisches Museum/Hellenic Botanical Society, Berlin/Athens
28. Phitos D, Constantinidis T, Kamari G (2009) The red data book of rare and threatened plants of Greece2nd edn. Hellenic Botanical Society, Patras
29. Legakis A, Pafilis P, Parmakelis A (2015) Editorial. J Nat Hist 49:2–8

30. Daget J, Economidis PS (1975) Richesse spécifique de l'ichtyofaune de Macédoine orientale et de Thrace occidentale (Grèce). Bull Mus Natl Hist Nat Paris 346:81–84
31. Economou AN, Giakoumi S, Vardakas L, Barbieri R, Stoumboudi M, Zogaris S (2007) The freshwater ichthyofauna of Greece: an update based on a hydrographic basin survey. Mediterr Mar Sci 8:91–168
32. Bianco PG (1990) Potential role of the paleohistory of the Mediterranean and Paratethys basins on the early dispersal of Euro-Mediterranean freshwater fish. Ichthyol Explor Freshw 1:167–184
33. Economidis PS, Bănărescu PM (1991) The distribution and origins of freshwater fishes in the Balkan peninsula, especially in Greece. Int Rev Gesamten Hydrobiol 76:257–283
34. Maurakis EG, Economidis PS (2001) Reconstructing biogeographic relationships of river drainages in Peloponnessuos, Greece using distributions of freshwater cyprinid fishes. Bios 6:125–132
35. Reyjol Y, Hugueny B, Pont D, Bianco PG, Beier U, Caiola N, Casals F, Cowx I, Economou AN, Ferreira T, Haidvogl G, Noble R, de Sostoa A, Vigneron T, Virbickas T (2007) Patterns in species richness and endemism of European freshwater fish. Glob Ecol Biogeogr 16:65–75
36. Zogaris S, Economou A, Dimopoulos P (2009) Ecoregions in the Southern Balkans: should they be revised? Environ Manag 43:682–697
37. Zogaris S, Legakis A, Rejyol Y, Chatzinikolaou Y, Dimopoulos P, Economou AN (2009) Freshwater biogeographic units in Greece: where to draw the lines? 11th International Congress on the Zoogeography and Ecology of Greece and Adjacent Regions-ICZEGAR, proceedings, 21–25 September 2009, Herakleion, p 204
38. Mazaris AD, Moustaka-Gouni M, Michaloudi E, Bobori DC (2010) Biogeographic patterns of freshwater micro and macroorganisms: a comparison between phytoplankton, zooplankton and fish in the eastern Mediterranean. J Biogeogr 37(7):1341–1351
39. Economou AN, Zogaris S, Vardakas L, Koutsikos N, Chatzinikolaou Y, Kommatas D, Kapakos Y, Giakoumi S, Oikonomou E, Tachos V (2016) Developing policy-relevant river fish monitoring in Greece: insights from a nation-wide survey. Mediterr Mar Sci 171:302–322
40. Illies J (1967, 1978) Limnofauna Europaea. Gustav Fisher Verlag, Stuttgart
41. Tierno de Figueroa JM, López-Rodríguez MJ, Fenoglio S, Sánchez-Castillo P, Fochetti R (2013) Freshwater biodiversity in the rivers of the Mediterranean Basin. Hydrobiologia 719 (1):37–186
42. Csabai Z, Soos N, Berchi GM, Cianferoni F, Boda P, Mora A (2017) Aquatic and semiaquatic Heteroptera (Nepomorpha and Gerromorpha) fauna of Greek holiday islands (Rhodes, Crete and Corfu) with first records of three species from Europe and Greece. Zootaxa 4231(1):51–69
43. Bailey RG (2002) Ecoregion-based design for sustainability. Springer, New York, NY
44. Loveland TR, Merchant JM (2004) Ecoregions and ecoregionalization: geographical and ecological perspectives. Environ Manag 34:(1): S1–(1):S13
45. Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R, Hansen M, et al. (2017) An ecoregion-based approach to protecting half the terrestrial realm. Bioscience. doi:10.1093/biosci/bix014
46. Bohn U, Gollub G, Hettwer C, Neuhäuslová Z, Raus T, Schlüter H, Weber H (2004) Map of the natural vegetation of Europe, scale 1:2.500.000, interactive CD-ROM – explanatory text, legend, maps. Landwirtschaftsverlag, Münster
47. Mavrommatis GN (1980) The bioclimate of Greece: relationships between climate and vegetation – bioclimatic maps. Institute for Forestry Research, Athens. (in Greek)
48. Triantis KA, Mylonas M (2009) Greek islands, biology. In: Gillespie R, Glague DA (eds) Encyclopedia of islands. University of California Press, Los Angeles, CA
49. Collier RELI, Leeder MR, Jackson JA (1995) Quaternary drainage development, sediment fluxes and extensional tectonics in Greece. In: Lewin J, Macklin MG, Woodward JC (eds) Mediterranean Quaternary river environments. A.A. Balkema, Rotterdam, pp 31–44

50. Higgins MD, Higgins R (1996) A geological companion to Greece and the Aegean. Cornell University Press, New York, NY
51. Skoulikidis N, Economou AN, Gritzalis KC, Zogaris S (2009) Rivers of the Balkans. In: Tockner K, Uehlinger U, Robinson CT (eds) Rivers of Europe. Elsevier Academic Press, Amsterdam
52. Valakos S, Pafilis P, Sotiropoulos K, Lymberakis P, Maragou P, Foufopoulos J (2008) Amphibians and reptiles of Greece. Chimaira Editions, Frankfurt-am-Main
53. Allen DH (2001) Mediterranean ecogeography. Pearson Education, London
54. Tselepedakis IG, Theoharatos GA (1989) A bioclimatic classification of the Greek area. Theor Appl Climatol 40:147–153
55. Baltas EA (2008) Climatic conditions and availability of water resources in Greece. Int J Water Resour D 24(4):635–649
56. Markonis Y, Batelis SC, Dimakos Y, Moschou E, Koutsoyiannis D (2016) Temporal and spatial variability of rainfall over Greece. Theor Appl Climatol. doi:10.1007/s00704-016-1878-7
57. Skoulikidis NT, Vardakas L, Karaouzas I, Economou AN, Dimitriou E, Zogaris S (2011) Assessing water stress in a Mediterranean lotic system: insights from an artificially intermittent river in Greece. Aquat Sci 73:581–597
58. Barbieri R, Zogaris S, Kalogianni E, Stoumboudi M, Chatzinikolaou Y, Giakoumi S, Kapakos Y, Kommatas D, Koutsikos N, Tachos V, Vardakas L, Economou AN (2015) Freshwater fishes and lampreys of Greece: an annotated checklist. Monographs on marine sciences no. 8. Hellenic Center for Marine Research, Athens
59. Vanhove MPM, Economou AN, Zogaris S, Giakoumi S, Zanella D, Volckaert FA, Huyse T (2013) The Gyrodactylus (Monogenea, Gyrodactylidae) parasite fauna of freshwater sand gobies (Teleostei, Gobioidei) in their centre of endemism, with description of seven new species. Parasitol Res 113:653–668
60. Strid A, Tan K (1997) Flora Hellenica, vol I. University of Copenhagen, Koeltz
61. Georghiou K, Delipetrou P (2010) Patterns and traits of the endemic plants of Greece. Bot J Linn Soci 162:130–422
62. Trigas P, Panitsa M, Tsiftsis M (2013) Elevational gradient of vascular plant species richness and endemism in Crete – the effect of post-isolation mountain uplift on a continental island system. PLoS One 8:e59425
63. Blaženčić J, Stevanović B, Blaženčić Ž, Stevanović V (2006) Red data list of charophytes in the Balkans. Biol Conserv 15:3445–3457
64. Sarika M, Dimopoulos P, Yannitsaros A (2005) Contribution to the knowledge of the wetland flora and vegetation of Amvrakikos Gulf, W Greece. Willdenowia 35:69–85
65. Catsadorakis G, Paragamian K (2007) Inventory of the wetlands of the Aegean Islands: identity, ecological status and threats. WWF Greece, Athens. (in Greek)
66. Koumpli-Sovantzi L (1997) The charophyte flora of Greece. I Fl Medit 7:173–179
67. Manolaki P, Papastergiadou E (2013) The impact of environmental factors on the distribution pattern of aquatic macrophytes in a middle-sized Mediterranean stream. Aquat Bot 104:34–46
68. Douda J, Boublík K, Slezák M, Biurrun I, Nociar J, Havrdová A, Doudová J, Aćić S, Brisse H, Brunet J, Chytrý M, Claessens H, Csiky J, Didukh Y, Dimopoulos P, Dullinger S, FitzPatrick U, Guisan A, Horchler PJ, Hrivnak R, Jandt U, Kazcki Z, Kevey B, Landucci F, Lecomte H, Lenoir J, Paal J, Paternoster D, Pauli H, Pielech R, Rodwell JS, Roelandt B, Svenning J-C, Sibık J, Silc U, Skvorc U, Tsiripidis I, Tzonev RT, Wohlgemuth T, Zimmermann NE (2016) Vegetation classification and biogeography of European floodplain forests and alder carrs. Appl Veg Sci 19(1):147–163
69. Dimopoulos P, Zogaris S (2008) Vegetation and flora of riparian zones. In: Arizpe D, Mendes A, Rabaca J (eds) Sustainable riparian zones: a management guide. Generalitat Valenciana, Valencia, pp 66–82

70. Zogaris S, Chatzinikolaou Y, Dimopoulos P (2008) Riparian woodland flora in upland rivers of Western Greece. Mediterr Mar Sci 9(2):87–103
71. Coughlan NE, Kelly TC, Davenport J, Jansen MA (2017) Up, up and away: bird-mediated ectozoochorous dispersal between aquatic environments. Freshw Biol. doi:10.1111/fwb.12894
72. Leeuwen CH, Velde G, Groenendael JM, Klaassen M (2012) Gut travellers: internal dispersal of aquatic organisms by waterfowl. J Biogeogr 39(11):2031–2040
73. Lopes-Lima M, Sousa R, Geist J, Aldridge D, Araujo R, Bergengren J, Bespalaja Y, Bódis E, Burlakova L, Van Damme D, Douda K, Froufe E, Georgiev D, Gumpinger C, Karatayev A, Kebapçi Ü, Killeen I, Lajtner J, Larsen B, Lauceri R, Legakis A, Lois S, Lundberg S, Moorkens E, Motte G, Nagel K, Ondina P, Outeiro A, Paunovic M, Prié V, Von Proschwitz T, Riccardi N, Rudzīte M, Rudzītis M, Scheder C, Seddon M, Şereflişan H, Simić V, Sokolova S, Stoeckl K, Taskinen J, Teixeira A, Thielen F, Trichkova T, Varandas S, Vicentini H, Zajac K, Zajac T, Zogaris S (2015) Conservation status of freshwater mussels in Europe: state of the art and future challenges. Biol Rev 92:572–607
74. Harzhauser M, Piller WE, Steininger FF (2002) Circum-Mediterranean Oligo-Miocene biogeographic evolution – the gastropods' point of view. Palaeogeogr Palaeocl 183:103–133
75. Gloer P, Fralnioski A, Pesic V (2010) The Bithynidae of Greece (Gasteropoda: Bithynidae). J Conchol 40(2):179–187
76. Radea C (2011) A new species of hydrobiid snails (Mollusca, Gastropoda, Hydrobiidae) from central Greece. ZooKeys 138:53–64
77. Radea C, Parmakelis A, Papadogiannis V, Charou D, Triantis KA (2013) The hydrobioid freshwater gastropods (Caenogastropoda, Truncatelloidea) of Greece: new records, taxonomic re-assessments using DNA sequence data and an update of the IUCN red list categories. ZooKeys 350:1–20
78. Jäch MA, Avtzis ND (1998) Check list of the Dryopidae, Elmidae and Hydraenidae (Coleoptera) of Greece. Entomol Hell 12:13–17
79. Trichas A (1996) Ecology and biogeography of the ground Coleoptera in the south Aegean area. Doctorate dissertation. University of Crete, Heraklion
80. Legakis A, Maragou P (2009) Greek red data book of threatened fauna. Hellenic Zoological Society, Athens
81. Malicky H (1979) The caddisflies (Insecta, Trichoptera) of the Ionian Islands. Biol Gallo-Hell 8:141–145
82. Sfenthourakis S, Legakis A (2001) Hotspots of endemic terrestrial invertebrates in southern Greece. Biodivers Conserv 10:1387–1417
83. Welter-Schultes FW (2000) The paleogeography of late Neogene central Crete inferred from the sedimentary record combined with Albinaria land snail biogeography. Palaeogeogr Palaeoclimatol Palaeoecol 157:27–44
84. Solà E, Sluys R, Gritzalis K, Riutort M (2013) Fluvial basin history in the northeastern Mediterranean region underlies dispersal and speciation patterns in the genus Dugesia (Platyhelminthes, Tricladida, Dugesiidae). Mol Phylogenet Evol 66:877–888
85. Christodoulou M, Anastasiadou C, Jugovic J, Tzomos T (2016) Freshwater shrimps (Atyidae, Palaemonidae, Typhlocarididae) in the broader Mediterranean region: distribution, life strategies, threats, conservation challenges and taxonomic issues. In: Kawai T, Cumberlidge N (eds) A global overview of the conservation of freshwater decapod crustaceans. Springer, Cham, pp 199–236
86. Hupało K, Mamos T, Olszewska W, Wysocka A, Karaouzas I, Plaiti W, Michał Grabowski M (2015) Diversity and origin of freshwater gammarids from Crete and Peloponnese – preliminary results. In: Poulakakis N et al. (eds) Abstracts of the International Congress on the Zoogeography and Ecology of Greece and Adjacent Regions, 13th ICZEGAR, 7–11 October 2015, Irakleio, Crete, Greece. Hellenic Zoological Society, Irakleio

87. Karaouzas I, Gritzalis KC (2006) Local and regional factors determining aquatic and semi-aquatic bug (Heteroptera) assemblages in rivers and streams of Greece. Hydrobiologia 573:199–212
88. Karaouzas I, İncekara Ü (2011) First record of the genus Berosus (Coleoptera: Hydrophilidae) in Crete island, Greece. Entomol Hell 20:69–74
89. Karaouzas I (2013) The larvae of the Aegean endemic caddisflies Hydropsyche debirasi Malicky 1974 and Hydropsyche kleobis Malicky 2001 (Trichoptera: Hydropsychidae) with notes on their ecology and zoogeography. Zootaxa 3636(4):472–477
90. Płóciennik M, Karaouzas I (2014) The Chironomidae (Diptera) fauna of Greece: zoogeographical distributions and patterns, taxalist and new records. Ann Limnol-Int J Lim 50:19–34
91. Bauernfeind E (2003) The mayflies of Greece (Insecta: Ephemeroptera) – a provisional check-list. Research update on Ephemeroptera and Plecoptera. University of Perugia, Perugia, pp 99–107
92. Karaouzas I, Adriopoulou A, Kouvarda T, Muranyi D (2016) An annotated checklist of the Greek stonefly fauna (Insecta: Plecoptera). Zootaxa 4111:301–333
93. Argyroudi A, Chatzinikolaou Y, Poirazidis K, Lazaridou M (2009) Do intermittent and ephemeral Mediterranean rivers belong to the same river type? Aquat Ecol 43:465–476
94. Skoulikidis NT, Karaouzas I, Gritzalis KC (2008) Identifying key environmental variables structuring benthic fauna for establishing a biotic typology for Greek running waters. Limnologica 39:55–66
95. Radea C, Parmakelis A, Giokas S (2016) Myrtoessa hyas, a new valvatiform genus and a new species of the Hydrobiidae (Caenogastropoda, Truncatelloidea) from Greece. ZooKeys 640:1–18
96. Olden JD, Kennard MJ, Leprieur F, Tedesco PA, Winemiller KO, García-Berthou E (2010) Conservation biogeography of freshwater fishes: recent progress and future challenges. Divers Distrib 16(3):496–513
97. Dias MS, Oberdorff T, Hugueny B, Leprieur F, Jézéquel C, Cornu JF, Brosse S, Grenouillet G, Tedesco PA (2014) Global imprint of historical connectivity on freshwater fish biodiversity. Ecol Lett 17(9):130–1140
98. Geiger MF, Herder F, Monaghan MT, Almada V, Barbieri R, Bariche M, Berrebi P, Bohlen J, Casal-Lopez M, Delmastro GB, Denys GPJ, Dettai A, Doadrio I, Kalogianni E, Kärst H, Kottelat M, Kovačić M, Laporte M, Lorenzoni M, Marčić M, Özuluğ M, Perdices A, Perea S, Persat H, Porcelotti S, Puzzi C, Robalo J, Šanda R, Schneider M, Šlechtová V, Stoumboudi M, Walter S, Freyhof J (2014) Spatial heterogeneity in the Mediterranean biodiversity hotspot affects barcoding accuracy of its freshwater fishes. Mol Ecol Resour 14(6):1210–1221
99. Tsigenopoulos CS, Berrebi P (2000) Molecular phylogeny of North Mediterranean freshwater barbs (genus Barbus: Cyprinidae) inferred from cytochrome b sequences: biogeographic and systematic implications. Mol Phylogenet Evol 14(2):165–179
100. Petit G (1930) Remarques sur la distribution geographique des poisons d'eau douce des Balkans. C R Soc Seances Soc Biol Fil 59:77–82
101. Smith KG, Darwall WRT (eds) (2006) The status and distribution of freshwater fish endemic to the Mediterranean Basin. IUCN, Gland
102. Froese R, Pauly D (eds) (2000) FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Laguna
103. Šanda R, Vukic J, Choleva L, Krízek J, Sedivá A, Shumka S, Wilson IF (2008) Distribution of loach fishes (Cobitidae, Nemacheilidae) in Albania, with genetic analysis of populations of Cobitis ohridana. Folia Zool 57(1/2):42
104. Vukić J, Ulqini D, Šanda R (2017) Occurrence of Knipowitschia goerneri Ahnelt, 1991 (Gobiidae) in southern Albania confirmed with molecular tools. J Appl Ichthyol 33(2):284–290
105. Bobori DC, Economidis PS (2006) Freshwater fishes of Greece: their biodiversity, fisheries and habitats. Aquat Ecosyst Health Manage 9:407–418

106. Pafilis P, Valakos SD (2012) Amphibians and reptiles of Greece: guide to identification. Patakis, Athens. (in Greek)
107. Sotiropoulos, K. (2004) Study on the variation of the genus Triturus (Amphibia, Urodela) in Greece, based on biochemical, morphological and ecological criteria. Doctoral Thesis. National and Kapodistrian University of Athens, Dept. of Biology, Section of Zoology and Marine Biology, Athens
108. Foufopoulos J, Ives AR (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. Am Nat 153:1–25
109. Handrinos G, Akriotis T (1997) Birds of Greece. Christopher Helm, London
110. Simaiakis SM, Dretakis M, Barboutis C, Katritis T, Portolou D, Xirouchakis S (2012) Breeding land birds across the Greek islands: a biogeographic study with emphasis on faunal similarity, species–area relationships and nestedness. J Ornithol 153(3):849–860
111. Catsadorakis G, Onmuş O, Bugariu S, Gül O, Hatzilacou D, Hatzofe O, Malakou M, Michev T, Naziridis T, Nikolaou H, Rudenko A (2015) Current status of the Dalmatian pelican and the great white pelican populations of the Black Sea/Mediterranean flyway. Endanger Species Res 27(2):119–130
112. Green AJ, Elmberg J (2014) Ecosystem services provided by waterbirds. Biol Rev 89(1):105–122
113. Stuart AJ, Lister AM (2007) Patterns of Late Quaternary megafaunal extinctions in Europe and northern Asia. Cour Forsch Inst Senckenberg 259:287–297
114. Van der Geer A, Dermitzakis M, De Vos J (2006) Crete before the Cretans: the reign of dwarfs. Pharos 13:121–132
115. De Vos J, van den Hoek Ostende LW, van den Bergh GD (2007) Patterns in insular evolution of mammals: a key to island palaeogeography. In: Renema W (ed) Biogeography, time, and place: distributions, barriers, and islands. Springer, Dordrecht
116. Blondel J (2008) On humans and wildlife in Mediterranean islands. J Biogeogr 35:509–518
117. Sfikas G (1985) Greek nature through the ages. Mikri Vivliothiki, Athens. (in Greek)
118. Voultsiadou E, Tatolas A (2005) The fauna of Greece and adjacent areas in the Age of Homer: evidence from the first written documents of Greek literature. J Biogeogr 32 (11):1875–1882
119. Masseti M (2012) Atlas of terrestrial mammals of the Ionian and Aegean islands. Walter de Gruyter, Berlin
120. Karandinos M, Paraschi L (1992) The red data book of threatened vertebrates of Greece. Hellenic Zoological Society and Hellenic Ornithological Society, Athens
121. Halley D, Rosell F, Saveljev A (2012) Population and distribution of Eurasian beaver (Castor fiber). Balt For 18:168–175
122. Catsadorakis G, Källander H (eds) (2010) The Dadia-Lefkimi-Soufli Forest National Park, Greece: biodiversity, management and conservation. WWF Greece, Athens
123. Perissoratis C, Conispoliatis N (2003) The impacts of sea-level changes during latest Pleistocene and Holocene times on the morphology of the Ionian and Aegean Seas (SE Alpine Europe). Mar Geol 196:145–156
124. Oikonomou A, Leprieur F, Leonardos ID (2014) Biogeography of freshwater fishes of the Balkan Peninsula. Hydrobiologia 738(1):205–220
125. Atalay I (2002) Ecoregions of Turkey. Ministry of Forestry, Publication n. 163, Ankara
126. Lykousis V, Karageorgis AP, Chronis GT (2005) Delta progradation and sediment fluxes since the last glacial in the Thermaikos Gulf and the Sporades Basin, NW Aegean Sea, Greece. Mar Geol 222–223:381–397
127. Kottelat M, Freyhof J (2007) Handbook of European freshwater fishes. Kottelat, Cornol and Freyhof, Berlin
128. Bianco PG (1986) The zoogeographic units of Italy and Western Balkans based on cyprinid species ranges (Pisces). Biol Gallo-Hell 12:291–299
129. Stierandová S, Šanda R, Vasil'eva ED, Zogaris S, Shumka S, Halačka K, Vetešník L, Nowak M, Stefanov T, Koščo J, Mendel J (2016) A multilocus assessment of nuclear and

mitochondrial sequence data elucidates phylogenetic relationships among European spirlins (Alburnoides, Cyprinidae). Mol Phylogenet Evol 94:479–491

130. Albrecht C, Wilke T (2008) Ancient Lake Ohrid: biodiversity and evolution. Hydrobiologia 615(1):103–140
131. Stephanidis A (1939) Freshwater fish of Attico-Beotia. Bull Phys Sci Fasc 50–51:49–60. (in Greek)
132. Lykousis V (2009) Sea-level changes and shelf break prograding sequences during the last 400ka in the Aegean margins: subsidence rates and palaeogeographic implications. Cont Shelf Res 29(16):2037–2044
133. Malicky H (1987) The miraculous island of Serifos-one possible key to understand the evolution of Mediterranean stream ecosystems. Biol Gallo-Hell 13:43–46
134. Welter-Schultes FW, Williams MR (1999) History, island area and habitat availability determine land snail species richness of Aegean islands. J Biogeogr 26(2):239–249
135. Schmitt T (2007) Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. Front Zool 4:11. doi:10.1186/1742-9994-4-11
136. Radea C, Louvrou I, Bakolitsas K, Economou-Amilli A (2017) Local endemic and threatened freshwater hydrobiids of Western Greece: elucidation of anatomy and new records. Fol Malac 25(1):3–13
137. Froufe E, Prié V, Faria J, Ghamizi M, Gonçalves DV, Gürlek ME, Karaouzas I, Kebapçi Ü, Şereflişan U, Sobral C, Sousa R, Teixeira A, Varandas S, Zogaris S, Lopes-Lima M (2016) Phylogeny, phylogeography, and evolution in the Mediterranean region: news from a freshwater mussel (Potomida, Unionida). Mol Phylogenet Evol 100:322–332
138. Christodoulou M, Antoniou A, Magoulas A, Koukouras A (2012) Revision of the freshwater genus Atyaephyra (Crustacea, Decapoda, Atyidae) based on morphological and molecular data. ZooKeys 229:53–110. doi:10.3897/zookeys.229.3919
139. Vukić J, Kovačić M, Zogaris S, Šanda R (2016) Rediscovery of Knipowitschia goerneri (Actinopterygii: Gobiidae) and its phylogenetic relationships with other northern Mediterranean Knipowitschia species. Ichthyol Explor Fres 26:363–372
140. Iliadou E, Kallimanis AS, Dimopoulos P, Panitsa M (2014) Comparing the two Greek archipelagos plant species diversity and endemism patterns highlight the importance of isolation and precipitation as biodiversity drivers. J Biol Res Thessalon 21:16
141. Vanhove MPM, Kovačić M, Zogaris S (2016) A distinct island population of threatened freshwater fish: to split or lump? Hydrobiologia 777:79–93
142. Rackham O, Moody J (1996) The making of the Cretan landscape. Manchester University Press, Manchester
143. Raus T (1991) Asia or Europe? – the phytogeographical position of the Karpathos archipelago (SE Aegean, Greece). Fl Veg Mundi 9:301–310
144. Creutzburg N (1963) Paleogeographic evolution of Crete from Miocene till our days. Cret Ann 15:336–342
145. Dermitzakis MD, Papanikolaou D (1981) Paleogeography and geodynamics of the Aegean region during the Neogene. Ann Geol Pays Hell 4:245–289
146. Legakis A (1987) Primary zoogeographic analysis of Crete. Biol Gallo-Hell 13:133–136
147. Markonis Y, Angelakis AN, Christy J, Koutsoyiannis D (2016) Climatic variability and the evolution of water technologies in Crete, Hellas. Water Hist 8:137–157. doi:10.1007/s12685-016-0159-9
148. Soukissian T, Hatzinaki M, Korres G, Papadopoulos A, Kallos G, Anadranistakis E (2007) Wind and wave atlas of the Hellenic seas. Hellenic Centre for Marine Research, Anavissos
149. Barbieri R, Stoumboudi MT, Giakoumi S, Kapakos Y, Skoulikidis N, Kalogianni E (2013) The fish fauna of the inland waters of Crete Island. 15th Panhellenic Ichthyological Congress, Thessaloniki, 10–13 October 2013. (in Greek with English abstract)
150. Legakis A, Kypriotakis Z (1994) A biogeographic analysis of the island of Crete, Greece. J Biogeogr 21:441–445

151. Stoumboudi MT, Kottelat M, Barbieri R (2006) The fishes of the inland waters of Lesbos Island, Greece. Icthyol Explor Freshw 17(2):129–146
152. Bianco PG, Ahnelt H, Economidis PS (1996) The freshwater fish from eastern and large Mediterranean islands with comments on their safety status. Acta Univ Carol 40:45–60
153. Davis PH (1965) Flora of Turkey and the east Aegean Islands, vol 1. Edinburgh University Press, Edinburgh
154. Fattorini S (2002) Biogeography of the tenebrionid beetles (Coleoptera, Tenebrionidae) on the Aegean Islands (Greece). J Biogeogr 29:49–67
155. Hausdorf B, Hennig C (2005) The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. Biol J Linn Soc 84:785–795
156. Geldiay R, Balik S (1999) Freshwater fishes of Turkey. Ege Universitesi Basimevi, Bornova-Izmir. (in Turkish)
157. Greuter W (1979) The flora and phytogeography of Kastellorizo (Dhodhekanisos, Greece). 1. An annotated catalogue of the vascular plant taxa. Willdenowia 8(3):531–611
158. Constantinidis T (2013) The flora of the Kastellorizo island group (East Aegean Islands, Greece): new records and comments. Fl Medit 23:69–86
159. Koutsikos N, Zogaris S, Vardakas L, Tachos V, Kalogianni E, Šanda R, Chatzinikolaou Y, Giakoumi S, Economidis PS, Economou AN (2012) Recent contributions to the distribution of the freshwater ichthyofauna in Greece. Mediterr Mar Sci 13(2):268–277
160. Higgins JV, Bryer MT, Khoury ML, Fitzhugh TW (2005) A freshwater classification approach for biodiversity conservation planning. Conserv Biol 19:432–445
161. Forman RT (1995) Land mosaics: the ecology of landscapes and regions. Island Press, Washington DC
162. Blackmore S (1996) Knowing the Earth's biodiversity: challenges for the infrastructure of systematic biology. Science 274(5284):63
163. Darwall WRT, Carrizosa S, Numa C, Barrios V, Freyhof J, Smith K (2014) Freshwater key biodiversity areas in the Mediterranean Basin hotspot: informing species conservation and development planning in freshwater ecosystems. IUCN, Cambridge
164. Zenetos A, Pancucci-Papadopoulou MA, Zogaris S, Papastergiadou E, Vardakas AL, Aligizaki K, Economou AN (2009) Aquatic alien species in Greece (2009): tracking sources, patterns and effects on the ecosystem. J Biol Res Thessalon 12:135–172
165. Vanhove MPM, Economou AN, Zogaris S, Giakoumi S, Kalogianni E, Volckaert FAM, Huyse T (2011) Phylogenetics and biogeography of Balkan 'sand gobies' (Teleostei: Gobiidae): vulnerable species in need of taxonomic revision. Biol J Linn Soc 105:73–91
166. Hartshorne R (1958) The concept of geography as a science of space, from Kant and Humboldt to Hettner. Ann Assoc Am Geogr 48(2):97–108
167. McMahon G, Wiken EB, Gauthier DA (2004) Towards a scientifically rigorous basis for developing mapped ecological regions. Environ Manag 34:111–124
168. Vlami V, Kokkoris IP, Zogaris S, Cartalis C, Kehayias G, Dimopoulos P (2017) Cultural landscapes and attributes of "culturalness" in protected areas: an exploratory assessment in Greece. Sci Total Environ 595:229–243
169. Kyriazi P, Kornilios P, Nagy ZT, Poulakakis N, Kumlutaş Y, Ilgaz C, Avcı A, Göçmen B, Lymberakis P (2013) Comparative phylogeography reveals distinct colonization patterns of Cretan snakes. J Biogeogr 40:1143–1155
170. Skoulikidis N, Lampou A, Karaouzas I, Gritzalis K, Zogaris S (2014) Stream ecological assessment on an Aegean island: insights from an exploratory application on Samothraki (Greece). Fresen Environ Bull 23(5):1173–1182
171. Malicky H (2005) Die Köcherfliegen Griechenlands. Denisia 17:1–240