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► To cite this version:

Jan Perret, Océane Cobelli, Adrien Taudière, Julien Andrieu, Yildiz Aumeeruddy-Thomas, et al. Time to refine the geography of biodiversity hotspots by integrating molecular data: The Mediterranean Basin as a case study. *Biological Conservation*, 2023, 284, pp.110162. 10.1016/j.biocon.2023.110162 . hal-04132081

HAL Id: hal-04132081

<https://hal.science/hal-04132081>

Submitted on 11 Aug 2023

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Time to refine the geography of biodiversity hotspots by integrating molecular data: The Mediterranean Basin as a case study

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ARTICLE INFO

Keywords:

Conservation priorities
Data mining
DNA barcoding
Endemism
Marine conservation
Molecular taxonomy

ABSTRACT

Three decades ago, worldwide biodiversity hotspots were founded on the distributions of continental plants and vertebrates. Here, we question the timeliness of refining the geography of hotspots by basing their definition on more taxa, thanks to the molecular data available for hyper-diverse organisms such as insects, fungi and marine biota.

To do so, we assess the temporal dynamic of molecular data acquisition and the geography of knowledge about lineages currently included or not into hotspot definition. Using the Mediterranean Basin hotspot as a case study, we examine the taxonomic and geographical facets of 175,828 DNA sequences distributed over 21,552 species, and 13,001 indexed biodiversity publications. We reveal a deeply fractured repartition of biodiversity research efforts within the hotspot regarding both barcoding efforts and publication activity, the northern side of the Mediterranean concentrating 84.16 % of the publications and 75.99 % of the public DNA sequences. In addition, 57.55 % of the sequences belong to lineages which were excluded from hotspots definition, with highly congruent geographical patterns among marine and continental lineages.

Based on this analysis, we suggest 1) using the uneven geography of knowledge to rebalance sampling efforts towards poorly known regions within the Mediterranean hotspot, 2) handling the molecular corpus of orphan lineages to feed forthcoming multi-taxa biodiversity assessment initiatives, in order to 3) refine the geography of

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<https://doi.org/10.1016/j.biocon.2023.110162>

Received 9 April 2023; Received in revised form 5 June 2023; Accepted 9 June 2023

Available online 17 June 2023

1. Introduction

More than 250 years of **taxonomic science*** (see Glossary in **Box 1**) probably catalogued only 1–10 % of the organisms living on Earth and in the oceans (Mora et al., 2011). Three decades ago, a minority of them, i. e. continental plants and vertebrates, served to draw the boundaries of biodiversity hotspots (now totalising 34 worldwide areas), propelling the Mediterranean Basin among the hottest places for conservation stakes (Myers et al., 2000; Mittermeier et al., 2005). The hotspots were defined as regions concentrating high levels of diversity, endemism and human footprint (Myers et al., 2000). This initiative was probably founded on 0.01–1 % of the total diversity on Earth, because it excluded the most species rich eukaryotic lineages of continental organisms, i. e. insects and fungi (Hawksworth and Lücking, 2017; Novotny et al., 2006; Mora et al., 2011), as well as the oceanic realm. Indeed, at the time, the global diversity patterns for these taxa were too poorly known to be used in the building of the hotspots.

Despite its inability to reflect the diversity of the branches of the tree of life, the hotspot initiative provided a priceless contribution for scientists and stakeholders, and introduced the first reading grid of the macro-geographical stakes for continental biodiversity conservation. The relevance of the biodiversity hotspot framework has been unambiguously highlighted by (1) its efficiency to provide conservation planners with ways to prioritise efforts (Myers, 2003; Selig et al., 2014), (2) its use as a network to develop a wide range of **DNA barcoding*** initiatives for biodiversity assessments (Lahaye et al., 2008) and to explore the evolutionary facets of biodiversity (Forest et al., 2007), and (3) its utility to provide predictive scenarios of biodiversity erosion in

response to the current global change (Malcolm et al., 2006; Bellard et al., 2014). Because of the taxa chosen to define the hotspots, all these contributions relied on the diversity of macro-organisms that were brought to the forefront, inexorably leaving out those that did not initially board on the *Myers' Arch*, with, at the top of the list, invertebrates, microorganisms and the marine biota.

In all ecosystems, both the spatial distribution and the temporal dynamics of macro-organisms are driven by intimate interactions with highly diversified communities of prokaryotes, invertebrates and micro-eukaryotes. Nested within large autotrophs and animals, this **nested biodiversity*** forms a holobiont with each of their hosts, and interacts as either physically linked mutualists and parasites, or free-living individuals using a macro-organism-based indirect pathway to feed or shelter. However, the diversity of hosted biota is highly variable among macro-organisms, ranging from extremely specialised species to interaction generalists (Bruns et al., 2002). Thus, there is a strong discrepancy between conservation stakes of macro- and micro-organisms. In continental ecosystems, this diversity mediates interactions among macro-organisms through ecological networks (Thébault and Fontaine, 2010). Considered as the functional backbone of continental ecosystems, ecological networks link above- and below-ground compartments of the ecosystems (Bardgett and Wardle, 2010), and represent powerful channels for fluxes and signals among interacting macro-organisms.

In marine environments, biotic interactions are multiplied due to the stronger tridimensional structure of the environment, particularly through the functional coupling between the pelagic (open water) and benthic (bottom) compartments that include energy and organic matter fluxes. Being the cradle of life on Earth, the oceans harbour **endemic***

Box 1 Glossary.

Agrobiodiversity: Specific or/and genetic biodiversity created by agricultural practices and agricultural ecosystems (e.g. interspecific agrobiodiversity of vegetable gardens, infraspecific agrobiodiversity of the olive tree).

Agroecosystem: A spatially and functionally coherent unit of agricultural activity, including the living and nonliving components involved in that unit as well as their interactions. Agroecosystems are thus developed and maintained by human social groups, through their distinctive practices, knowledge and know-how (e.g. forest gardens, oasis, etc.).

Anthropogenic: Generated by humans or their activities (e.g. anthropogenic greenhouse effect, human-mediated species niches).

DNA barcoding: Method consisting of taxonomically positioning a biological organism based on the analysis of the nucleotide sequence of one or several targeted well-conserved genes. Molecular barcodes depend on the considered lineage: the internal transcribed spacer (ITS) is considered as a universal molecular barcode for plants and fungi, while the mitochondrial cytochrome C oxidase subunit I gene (COI) is the most used marker for animals.

Endemism: Property of species whose natural distribution is restricted to a delimited area. The Mediterranean is one of the two main diversity hotspots of endemism, with tropical Andes.

Ethnoscience: Anthropological/ethnographic studies that aim to reconstruct what serves as science for human social groups that do not rely on academic science to think and act on the world (e.g. ethnobotany, ethnomycology).

Metabarcoding: Widely applied method in community ecology that consists of combining high throughput sequencing (HTS, also known as NGS for next-generation sequencing) methods and barcoding procedure to taxonomically position co-occurring organisms from a biotic sample, in order to characterise species assemblies.

Nested biodiversity: Notion used in ecology, particularly in network-based analyses, designing a set of organisms interacting with another organism of different nature, generally higher in size and establishing trophic links with these associated biotas.

NGS (Next Generation Sequencing): Set of methods consisting of paralleling the DNA sequencing of multiple organisms contained in a given sample. These approaches allow a massive production (up to millions of sequences per run) of short sequences which require the use of Bio-informatic pipelines to be taxonomically assigned.

Taxonomy: Discipline consisting of describing living organisms based on the analysis of their morphological, molecular, chemical and/or ecological traits, positioning them within the tree of life, and assigning them the corresponding validated names.

marine phyla (e.g. 13–16 over 33–39 total metazoan phyla depending on authors) and still host the first metazoan groups that appeared on the planet (Ruggiero et al., 2015; Templado et al., 2010). Their long evolutionary history paralleled that of many microorganisms with which they have contracted intricate relationships. Today's resulting holobionts (e.g. bacteriosponges, reef-building corals; Cardini et al., 2015; Pita et al., 2018) take part in extremely diversified “nested ecosystems” and many of them are keystone and engineer species of highly diversified, productive and emblematic ecosystems, such as coral reefs of ultra-oligotrophic Pacific waters, or chemosynthetic communities of deep-sea hydrothermal vents. Many of the littoral marine ecosystems, including some unique in their functioning and structuring (Boudouresque et al., 2006, 2014), are strongly depending on these biotic interactions, such as the emblematic coralligenous habitat or dark submarine caves (Ballesteros, 2006; Harmelin et al., 1985).

Beyond their pivotal role for ecosystem functioning, continental and marine lineages forming the macro-organisms' holobionts share singular diversity patterns. Thus, invertebrates, fungi and microbes display astonishing alpha diversity and high proportions of cryptic and semi-cryptic species (e.g. fungi: Fryssouli et al., 2020; Bidaud et al., 2021; eukaryotic plankton: de Vargas et al., 2015), that make morphologically-based description insufficient for species identification. This lack of morphological signature makes these organisms perfect candidates for using DNA barcoding to more accurately document their diversity (DeSalle and Goldstein, 2019; see also Richard et al., 2015 for a case study of emblematic fungi).

In this paper, our aim was to assess whether the knowledge on biodiversity acquired since Myer's initiative allows to 1) enlarge the taxonomic basis of hotspot definition in order to 2) refine the geography of conservation stakes within hotspots. We based our analysis on scientific publications and barcoding data available in public databases, a corpus which was largely absent from Myer's toolbox in the early 2000th. We used the Mediterranean basin as a case study because this region concentrates a lot of data on biodiversity for a wide range of taxa (Daru and Rodriguez, 2023), and because there is an extensive network of taxonomists who could easily give us feedback on our methods and results.

We followed a three-step process. First, we analysed the temporal dynamics of acquisition and the taxonomic assignment of 175,828 DNA sequences distributed over 21,552 species, and 13,001 indexed biodiversity publications. In this analysis, we considered all continental taxa included in Myer's publication, two hyper-diversified groups of organisms (i.e. insects and fungi) and three lineages of marine taxa. Secondly, we examined the geography of these biodiversity records, by testing the spatial congruence between publications and DNA sequences on the one hand, and among taxa on the other hand. Finally, we propose a possible framework to handle the existing and forthcoming molecular corpus from a large taxonomic range to refine the cartography of conservation stakes within hotspots.

2. The Mediterranean hotspot concentrates diversity, endemism and strong anthropic footprint on biodiversity

The Mediterranean Basin is considered as one of the most prolific continental diversity hotspots (Myers et al., 2000) and a hotspot for marine endemism (Selig et al., 2014; Coll et al., 2010; Lejeune et al., 2010). It hosts an exceptional concentration of species, including for example 10 % and 16.9 % of Earth's continental and marine flora respectively (Médail and Quezel, 1997; Bianchi and Morri, 2000). This region, and particularly its western part, is one of the main clusters of observation records of macro-organisms worldwide (Daru and Rodriguez, 2023).

Since the beginning of the Cenozoic, the Mediterranean area accumulated continental organisms of highly contrasted biogeographical origins (e.g. Mediterranean paleo-endemic, tropical, Holarctic, Urano-Turanian, Saharo-Arabian), which met and evolved in a matrix of

highly diverse habitats resulting from a complex geological history. Similarly, but for different reasons, the marine Mediterranean biota is extremely diverse. During the Mesozoic, a large ocean known as the Tethys united the Atlantic and Indo-Pacific realms. Geological events progressively disconnected the Mediterranean Sea from the two oceans, culminating in a period of total sea closure (the Messinian salinity crisis, 5.97–5.33 Ma). Later, the reopened connection to the Atlantic filled the Mediterranean Basin again and the successive glacial cycles caused repeated immigration waves of marine organisms (the so-called ‘diversity pump’ from the Atlantic) that produced an unusually rich marine life for such a small and enclosed sea (0.82 % of the world ocean surface but 4–18 % of all marine species; Bianchi and Morri, 2000; Lejeune et al., 2010). Therefore, the Mediterranean Sea is considered as a factory producing endemics (Bianchi and Morri, 2000; Coll et al., 2010; Lejeune et al., 2010). This scenario led to the current coexistence in the Mediterranean Sea of marine biota of highly contrasted biogeographical origins (cold vs temperate vs subtropical; Indo-Pacific vs Atlantic vs paleo-endemic). Thus, Mediterranean conditions acted as a breeding ground for exceptionally high levels of endemism, both above and below the sea level (Blondel and Aronson, 1999; Selig et al., 2014; Médail et al., 2019).

Despite their high level of diversity and endemism, the dominant seascapes and landscapes within the Mediterranean Basin intriguingly rely on a reduced number of key species that originate from the area's tormented history. The paleo-endemic seagrass *Posidonia oceanica*, a relic from the Tethys Ocean, is the main support to life in the low nutrient high chlorophyll Mediterranean marine ecosystems through the functional support it provides, e.g. the main source of water oxygenation and an interaction hub in the food web (Boudouresque et al., 2006). Similarly, evergreen oaks (*Quercus ilex* s.l., *Q. suber* and *Q. coccifera* s.l.) form monodominant forests that cover millions of hectares around the Mediterranean Basin (Scarascia-Mugnozza et al., 2000), and play a pivotal trophic role by nourishing myriads of associated insects and fungi interacting within complex interaction networks (e.g. Ramírez-Hernández et al., 2014; Taudiere et al., 2015). From this systemic perspective, macro-organisms' endemism in the Mediterranean Basin determines and depends on interactions with a wide taxonomic range of nested endemic organisms (Rochet et al., 2011; Vereecken et al., 2010). From a conservation perspective, this highly interlinked architecture of ecological networks provides strong support for pursuing conservation strategies encompassing data from a large taxonomic pool, with particular attention on nested diversity.

The long-term history of the Mediterranean basin is inextricably related to human activity in the region. Millennia of human presence have profoundly altered the disturbance regime affecting Mediterranean ecosystems, especially since the Holocene (Roberts et al., 2019), by successively contributing to the extinction of the megafauna (Turvey, 2009) and altering natural wildfire cycles (Leys et al., 2014). The progressive establishment of a human-based disturbance regime has deeply shaped the spatial distribution and dynamics of biota, and has strongly influenced the composition and functioning of communities, from coastal to mountainous ecosystems (Blondel et al., 2010; Lestienne et al., 2020). This anthropogenic influence wove remarkable landscapes, made of patchy mosaics of highly valued habitats for biodiversity (EEC, 1992), including millions of hectares of man-made steady tree savannas, extending from the Iberian Peninsula to the Taurus mountains (Grove and Rackham, 2003; Rodríguez-Rojo et al., 2022), where evergreen oaks shelter hundreds of associated biotas (Taudiere et al., 2015). In these typical landscapes, 10,000 years of successive civilizations since the Neolithic contributed to increase a certain component of the Mediterranean biodiversity, by favouring traits adapting organisms to local environmental conditions. This occurred through the process of domestication, followed by the establishment of the agropastoral systems, and more recently through agriculture, farming and industrial uses (Blondel, 2006; Gros-Balthazard et al., 2020; Sineo and Speciale, 2022). At the scale of the Mediterranean basin, the diversity of such

anthropogenic systems (agroecosystems*) and their organisms (agrobiodiversity*) is still not fully described (Box 2). These resources, whether considered as a pool of varieties, a set of patentable genes or a precious corpus of local knowledge (TEK, traditional ecological knowledge), constitute one of the major facets of the current Mediterranean biodiversity (Box 2).

3. DNA barcoding-based knowledge, a taxonomic corpus that awaits to be handled? The Mediterranean as a case study

Over the last two decades, the emergence of a multitude of DNA barcoding initiatives resulted in an unprecedented accumulation of taxonomic data (Fig. 1b) that contributed to improve our knowledge on the distribution patterns for both marine and continental biodiversity. The first attempts to draw a global (coastal and pelagic) map of marine biogeographic realms were made (Longhurst, 2007; Spalding et al., 2007; Tittensor et al., 2010; Selig et al., 2014; Toonen et al., 2016), leading to the recent proposition of 30 distinct entities, based on the distribution of 65,000 species of animals and plants (i.e. much less than 10 % of known marine species; Costello et al., 2017). This has at last opened the possibility of conducting integrative marine-continental syntheses.

Since the turn of the millennium, field naturalists and molecular biology academics created collaborating networks to elucidate the overlooked diversity of poorly known lineages. This started with the use of quasi-universal or phylum-specific barcode markers, combined with standardised species recognition procedures, before moving towards an integrative science combining the morpho-/ecological analysis of organisms and their molecular signature. Integrative taxonomy has thus been successfully applied to resolve poorly known continental (e.g., insects: Jinbo et al., 2011; fungi: Zamora et al., 2018) and marine lineages (e.g. Gazave et al., 2012). Following more affordable sequencing costs and the rise of DNA sequencing as a powerful help for species discovery (Hebert et al., 2003; Hajibabaei et al., 2006), public molecular databases grew exponentially during the last two decades, doubling on average every 18 months according to GenBank (2023).

In this paper, we focused on the Mediterranean hotspot. We applied a data mining procedure to analyse 75,249 publications indexed in the Clarivate Analytics' Web of Science (WoS) database, and 23,301,464 DNA sequences deposited in NCBI's GenBank Nucleotide database (see Fig. S1 for a summary of the analysis process and Appendix 2 for a detailed description). For each taxa, we filtered the sequences to keep only the main markers used for taxonomic purposes, to be as representative as possible of the sequencing effort for each taxa (see Appendix 2 for details on the selected markers). We used the number of publications indexed in WoS and the number of sequences deposited in GenBank as proxies for the research effort and the taxonomic description effort, respectively. Thus, we were able to document the temporal dynamics and the geographical distribution of knowledge acquisition across the Mediterranean Basin for taxa included in the hotspot definition (i.e. continental plants, amphibians, reptiles, mammals and birds) and for six taxa that were excluded from it (i.e. fungi, diurnal butterflies, beetles, marine crustaceans, marine fishes and sponges).

For the eleven taxa we considered, the molecular corpus showed a continuous growth between 1996 and 2020, with a strong acceleration during the last decade as compared to the previous one (on average, 2944 and 13,255 sequences for our selected markers were deposited each year during the periods 2000–2009 and 2010–2020, respectively; Fig. 1a). Since 1996, 175,828 such DNA sequences taxonomically assigned to 21,552 species and geographically positioned within the Mediterranean Basin have been deposited in public databases, 99.39 % of which were deposited after Myers' designation of the biodiversity hotspots (Figs. 1b & S1). Interestingly, the proportion of molecular information related to organisms included in hotspot definition continuously decreased, from 60.27 % of the corpus in 2000 to becoming minority in 2011 and dropping to 41.91 % in 2020 (Fig. 1a). Currently, fungi are the most sequenced group of organisms (with 27.16 % of the deposited sequences), followed by terrestrial plants (18.41 %) and beetles (13.25 %; Fig. 1b & c).

In public DNA databases, the accumulated corpus concerns 8750 Mediterranean barcoded species of plants and vertebrates, including 31 % of the plant species and 82 % of the bird species expected in the

Box 2

Mediterranean agrobiodiversity.

The Mediterranean is both an ecological and social object, whose biodiversity has been largely shaped on different spatial and temporal scales by the mosaic of human societies over millennia of presence — especially significant outside the marine domain. We must go beyond the idea of an **anthropogenic*** impact as mere disturbance, pollution or destruction, however real and relevant. The anthropogenic legacy in the Mediterranean is more broadly characterised as the shaping, whether voluntary or not, of habitats and the living world through various knowledge and practices, whether in terms of the introduction or suppression of species or the transformation of environments at different scales.

By shaping, we do not only deal with the addition of species: human activity led to collateral increases and decreases in alpha, infraspecific and/or genetic biodiversity. This anthropogenic shaping of biodiversity covers all the gradients between the following two poles:

- Intentional: e.g. through domestication, the introduction of cultivated or bred species, micro-organisms, subsistence and botanical gardens and, ultimately, landscapes.
- Unintentional: for example, through the introduction and naturalisation of species (e.g. invasive exotic, companion species, feral crops), the admixture of divergent genepools of native species, the creation of biodiversity niches (ports, walls, human habitat), etc.

As such, a future line of work will be to focus on agrobiodiversity, a structuring facet of the Mediterranean. This agrobiodiversity is organised and hosted there by a wide range of **agroecosystems***. These socio-ecosystems are highly resilient as long as the localised knowledge and diversified practices of close interactions between the human groups living there and the natural component are maintained. In the Mediterranean, the published scientific production is driven by only two or three cultivated species and overwhelmingly by the olive tree, in contrast to the rich agrobiodiversity in the corresponding agroecosystems (Table S6).

This suggests integrating other forms of publications (grey literature, agronomic reports, etc.) to include agrobiodiversity in multi-taxa analysis. In particular, we are aiming at the environmental/ecological knowledge that the **ethnoscience*** have been working to make accessible over the last few decades, i.e. all the local knowledge of the inhabitants of the Mediterranean Basin about their living environments, local people being themselves shapers of agrobiodiversity, and also observers and descriptors of life as a whole - in a way that is different but as relevant as life sciences.

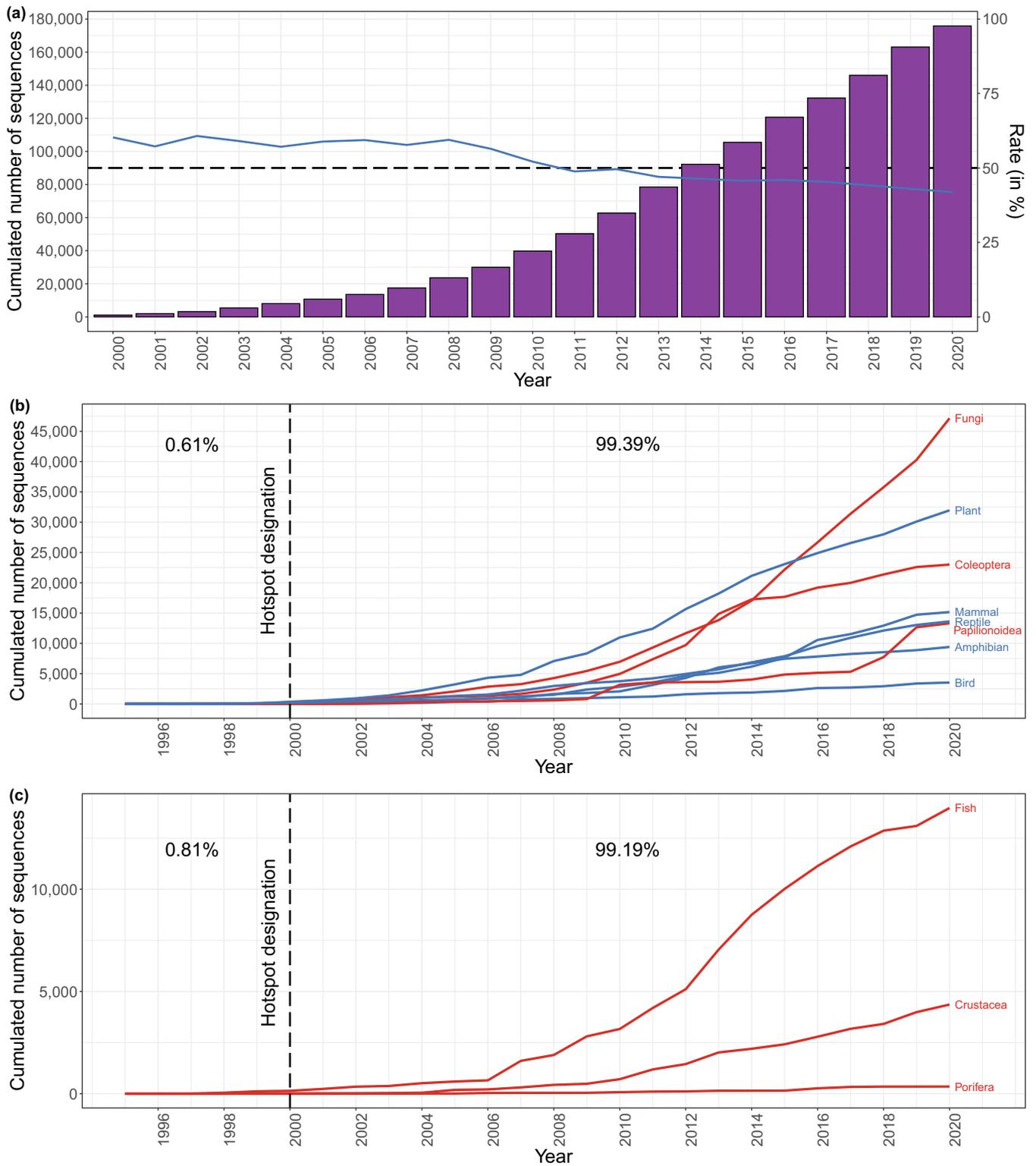


Fig. 1. Temporal dynamics of DNA sequencing for taxonomic purposes in the Mediterranean Basin. (a) Cumulated number of DNA sequences deposited in GenBank during the period 2000–2020 (purple bars), with the proportion of the sequences related to groups included in the definition of hotspots, i.e. continental plants and vertebrates (blue curve). (b) Detail of the number of sequences deposited in GenBank during the period 2000–2020 for continental taxa. The percentages indicated on (b) and (c) are the proportion of sequences acquired before and after the publication of Myers et al. (2000). Taxa shown in blue are those that were included in the definition of hotspots, and those shown in red are those that were excluded. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ecoregion based on published flora or fauna, and 100 % of the recorded species of reptiles, amphibians and mammals. For the other continental and marine lineages, the taxonomic diversity still awaits a synthesis at the scale of the ecoregion, so the number of occurring species is largely unknown. However, the molecular information is probably still far from complete for these lineages, as sequences are available in public databases for only 8077 species of fungi, 3416 species of beetles, 436 diurnal butterflies, 494 marine fishes, 291 marine crustaceans and 88 sponges. With the accelerating production of molecular-based taxonomic information (Fig. 1) and the development of promising **metabarcoding*** **NGS*** tools (see e.g. [Bidaud et al., 2021](#) for an example of using NGS for taxonomic assignment of old herbarium specimens) applied to a wide spectrum of biological material and environmental substrates, the generated data could feed large-scale biodiversity assessments, and thus contribute to effectively driving biological conservation strategies. However, this requires: 1) rethinking the vocation of these data; 2) considering their potential for developing taxonomically-enlarged biodiversity assessments, especially in hotspot areas; and 3) developing a way to combine the molecular corpus and the expert knowledge mobilised in Myers' initiative.

4. The Mediterranean hotspot is defined on a highly uneven geography of knowledge

The collectively shared representation of the continental biodiversity hotspots is that they are homogeneous. This is symbolised by the emblematic Fig. 1 in [Myers et al. \(2000\)](#), which shows a global map where 1) all hotspots display the same “temperature” (i.e. the same colour is used to represent all hotspots), and 2) each hotspot presents a “homogeneous and continuously diffused warming process” (i.e. the same colour covers homogeneously the entire ecoregion considered), without enclaves depicting for example a lack of available data or reporting about the uneven geographical patterns of the compiled data.

However, in the Mediterranean Basin, previously published taxon-centred syntheses provide finer views of this global representation and highlight the existence of uneven biodiversity stakes across the hotspot, such as the presence of nested sub-hotspots within the ecoregion (see for example [Médail and Quezel, 1997](#) and [Médail, 2022](#) for terrestrial vascular plants). To the best of our knowledge, similar representations are still lacking for most continental and marine biota. In this article, we document this geographical dimension of the accumulated corpus

related to biodiversity within the Mediterranean hotspot.

In NCBI's GenBank Nucleotide database, for the studied taxa and markers, the country of origin of the sequenced samples was available for only 55.88 % of the deposited sequences, varying from 54.79 % for marine organisms, to 49.65 % for macro-organisms included in hotspot definition, and up to 66.48 % for continental lineages (insects, fungi) not included in Myers' analysis. In other words, roughly one out of two deposited barcodes is unusable for contributing to reliable spatial meta-analysis. The analysis of geographically assigned data reveals a deeply fragmented pattern across the region. Indeed, the current geographical distribution of both the molecular data deposited in GenBank (used as a proxy for the available information regarding molecular-based taxonomy) and of the publications indexed in the WoS (used as a broad and integrated proxy for the research effort on biodiversity) illustrates neither a homogenous intensity of research nor of sequencing, but rather a contrasted pattern for both continental and marine organisms. On the continent, sequencing and publication corpus are highly congruent and reveal a highly unbalanced research effort. Since 1990, the northern side of the Mediterranean has concentrated 72.16 % of the publications (Figs. 2a, b & 3; Table 1) and 84.52 % of the deposited sequences (Figs. 2d, e & 3; Table 1). This marked contrast between the northern and southern shores is mainly driven by the disproportionately high contribution of four Northwestern countries (Spain followed by Italy and, to a lesser extent, France and Portugal) which together account for 64.53 % of the deposited sequences and 57.42 % of the publications (Fig. 3; Table 1). These well studied area contrast with the Balkans and northern Africa where molecular-based information (13.04 % of the corpus) and indexed publications (9.12 % of the corpus) are almost absent (see also [Médail and Baumeil, 2018](#) for narrow endemic plants; Fig. 3). Comprising Libya, Tunisia, Algeria and five countries in the Balkans (i.e. 25.97 % of the continental Mediterranean region) these two areas separate the north-western shore from the north-eastern, as two separated and intensively explored parts of the hotspot (Figs. 2a, b, d, & e, 3).

Similarly, the geography of research effort on marine species is highly contrasted; the northern part of the Mediterranean Basin concentrates most publications (Fig. 2c) and sequences (Fig. 2f), with data from the Adriatic Sea, the Aegean Sea and the Western Mediterranean accounting for 46.25 % of the publications while three countries (Turkey, Italy and France) account for 44.60 % of the deposited sequences (Fig. 2c). However, sequencing of marine biotas shows a

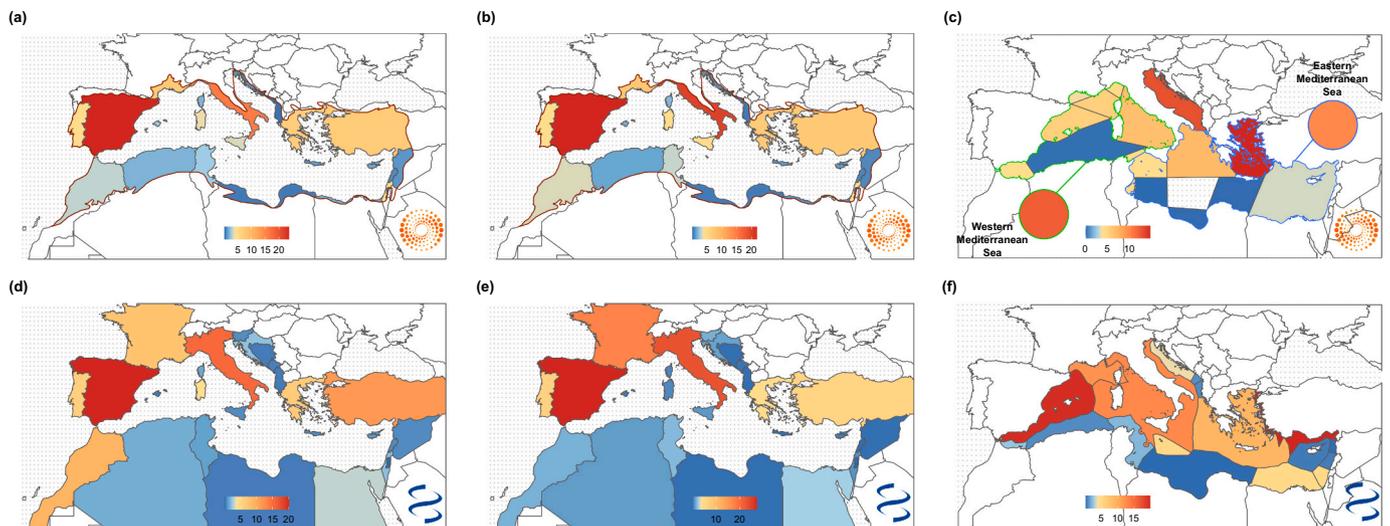


Fig. 2. Geographical distribution across the Mediterranean hotspot of the publications indexed in Clarivate Analytics' WoS database for continental lineages included (a) or not (b) in the hotspot definition, and for marine organisms (c). Geographical distribution across the Mediterranean hotspot of the DNA sequences deposited in NCBI's GenBank Nucleotide database for continental lineages included (d) or not (e) in the hotspot definition, and for marine organisms (f). The analysis is performed on data from the period 1990–2020.

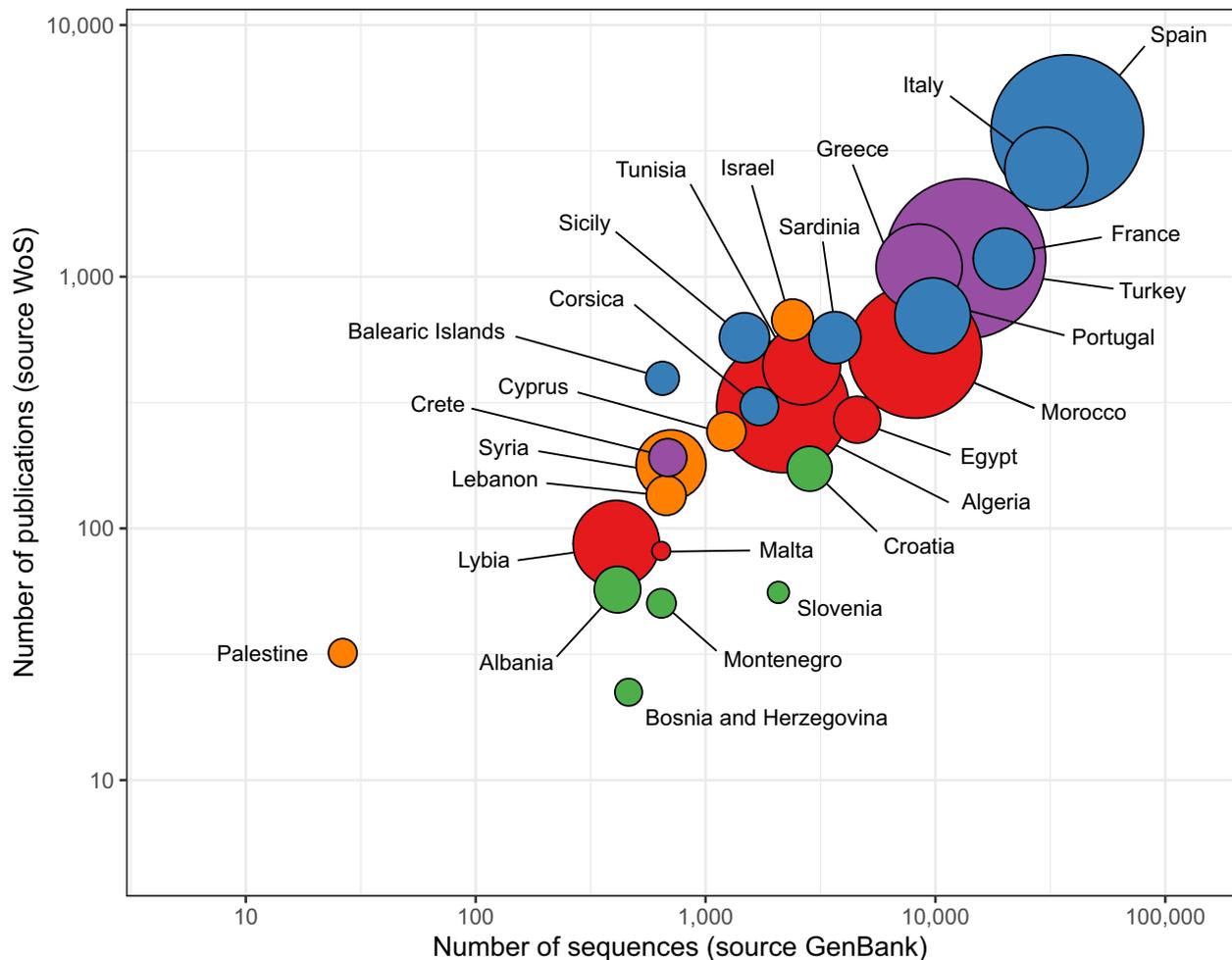


Fig. 3. Distribution of the 22 Mediterranean countries and the five largest islands according to the number of publications about Mediterranean biodiversity and the number of assigned DNA sequences* deposited in GenBank (only continental taxa are considered). The size of each circle indicates the area of terrestrial ecosystems under Mediterranean climate. Colours indicate the affiliation to the following geographical categories: blue (North West), purple (North East), green (Balkans), red (South), orange (Near East). The axes are in logarithmic scale.

*For continental vertebrates, diurnal butterflies (Rhopalocera), beetles (Coleoptera), continental plants (Embryophyta) and fungi (Dicaromycota). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

slightly more complex geographical pattern than for continental species, with three groups of minor contributors scattered across the basin (i.e. five countries in the Balkans, four countries from Morocco to Libya and three countries in the eastern area, Cyprus, Lebanon and Syria; Fig. 2f).

The uneven distribution of sequencing efforts is especially worrisome, as it creates the risk that these poorly known areas will remain largely overlooked in large-scale syntheses using the big data, due to their inability to provide valuable taxonomic information, as for instance for animals (sponges), plants (phytoplankton) and fungi with cryptic diversity. Therefore, the forthcoming global biodiversity syntheses should provide nuanced views of hotspots by explicitly representing the variation of available knowledge within their boundaries, based on the geography of the underlying biodiversity data (Fig. 2). Because poorly described areas are also imminently affected by global change (e.g. marine and continental ecosystems of the southern shore in the Mediterranean), there is an urgent need to prioritise biodiversity sampling in these “knowledge-cold” marine and continental areas within hotspots, notably by initiating ambitious barcoding programs.

5. Across the Mediterranean, both continental and marine organisms display highly congruent geographical patterns of taxonomic knowledge

Whether or not they belonged to lineages included in the Myers’ hotspot definition, the analysed taxa show a remarkably congruent geographical pattern of publications and sequencing effort (Table S1). The geographical distribution of the available corpus reveals three regional hotspots of both publication and sequencing for all eleven taxa (on land: Iberian Peninsula, Ligurian area, and north-eastern shore; at sea: the Adriatic, Aegean and Western Mediterranean seas), which strikingly contrast with poorly explored areas whatever the considered lineage (on land: the Balkans region, the five largest Mediterranean islands, and southern and south-eastern shores; at sea: Tunisian Plateau, Libyan Sea, Gulf of Sidra, and Algerian Basin).

In all Mediterranean countries, the number of articles published on continental taxa is very unevenly distributed among taxa (Fig. 4a; Table S3). Plants are by far the most studied taxa, with 14 countries where more than 50 % of the articles published on continental taxa deal with plants (up to 71 % in Bosnia and Herzegovina). The sequencing effort of continental organisms is more evenly distributed among taxa, with fungi being the most sequenced taxa in 12 countries, plants in 8 countries, followed by reptiles (two countries), mammals (two

Table 1

Geographical distribution of DNA sequences deposited in NCBI's GenBank Nucleotide database and publications indexed in Clarivate Analytics' WoS database across the Mediterranean Basin, for groups of organisms included in the definition of biodiversity hotspots (Myers et al., 2000) and for major groups of terrestrial (insects and fungi *pro parte*^a) and marine organisms (Porifera, Crustacea and fishes). Values in brackets indicate the percentage of the whole corpus we studied. For the number of publications and the associated percentages, it was taken into account that some publications deal with more than one taxa and more than one country. Marine organisms were not taken into account in this table because they were geographically assigned to marine regions and not countries.

Country (region)	Number of sequences			Number of publications		
	Vertebrates and plants sensu Myers et al.	Fungi, insects <i>pro parte</i> and marine organisms <i>pro parte</i>	Ratio (in %)	Vertebrates and plants sensu Myers et al.	Fungi and insects <i>pro parte</i>	Ratio (in %)
Portugal	4340 (2.50)	5392 (3.10)	48.77	585 (4.50)	71 (0.55)	0.89
Spain	15,148 (8.72)	26,149 (15.06)	36.05	3381 (26.00)	387 (2.98)	0.90
France	6503 (3.74)	16,997 (9.79)	26.42	1188 (9.14)	145 (1.12)	0.89
Italy	14,878 (8.57)	22,611 (13.02)	42.46	2643 (20.33)	387 (2.98)	0.87
North Western	40,869 (23.54)	71,149 (40.99)	37.05	6967 (53.59)	851 (6.55)	0.89
Croatia	1662 (0.95)	1714 (0.98)	46.91	157 (1.21)	18 (0.14)	0.90
Slovenia	638 (0.36)	1473 (0.84)	24.95	45 (0.35)	11 (0.08)	0.80
Montenegro	424 (0.24)	367 (0.21)	53.24	44 (0.34)	8 (0.05)	0.85
Albania	327 (0.18)	222 (0.12)	62.77	51 (0.39)	8 (0.06)	0.86
Bosnia and Herzegovina	334 (0.19)	122 (0.07)	78.08	20 (0.15)	2 (0.02)	0.91
Balkans	3385 (1.95)	3898 (2.24)	43.93	273 (2.10)	42 (0.32)	0.87
Algeria	1203 (0.69)	1116 (0.64)	58.37	259 (1.99)	24 (0.18)	0.92
Tunisia	965 (0.55)	1985 (1.14)	31.20	378 (2.91)	53 (0.41)	0.88
Malta	496 (0.28)	933 (0.53)	14.99	71 (0.55)	11 (0.08)	0.87
Egypt	2242 (1.29)	2982 (1.71)	48.53	248 (1.91)	17 (0.13)	0.94
Libya	327 (0.18)	104 (0.05)	75.30	74 (0.57)	8 (0.06)	0.90
Morocco	6728 (3.87)	1835 (1.05)	78.36	427 (3.28)	57 (0.44)	0.88
Southern	11,961 (6.89)	8955 (5.15)	57.87	1213 (9.33)	142 (1.09)	0.90
Greece	5401 (3.11)	5255 (3.02)	48.09	987 (7.59)	121 (0.93)	0.89
Turkey	8483 (4.88)	8307 (4.78)	50.53	1029 (7.91)	121 (0.93)	0.89
North Eastern	13,884 (7.99)	13,562 (7.81)	49.53	1903 (14.64)	226 (1.74)	0.89
Israel	1561 (0.89)	1541 (0.88)	48.84	581 (4.47)	69 (0.53)	0.89
Cyprus	807 (0.46)	487 (0.28)	60.92	220 (1.69)	21 (0.16)	0.91
Lebanon	599 (0.34)	152 (0.08)	78.84	127 (0.98)	12 (0.09)	0.91
Syria	593 (0.34)	146 (0.08)	81.50	160 (1.23)	13 (0.10)	0.92
Palestine	24 (0.01)	2 (0.001)	90.00	28 (0.22)	1 (0.007)	0.97
Near East	3584 (2.06)	2328 (1.34)	5693 (3.63)	988 (7.60)	107 (0.82)	0.90

^a For insects, only Coleoptera (beetles) and Rhopalocera (diurnal butterflies) were considered in the analysis; for fungi, the analysis was restricted to Dicyariomycota (including filamentous Ascomycota and Basidiomycota).

countries), amphibians (one country) and diurnal butterflies (one country; Fig. 4c; Table S2). For marine biota, fishes are by far the most studied taxa, with 63.64 % of indexed publications and 75.60 % of public DNA sequences. Fishes are also the most studied taxa in all marine regions and the most sequenced in all but one country (i.e. crustaceans account for 55.18 % of sequences from Spain). Interestingly, for both continental and marine organisms, the most studied taxa is broadly the same on the northern and southern shores of the Mediterranean Sea, despite the large North-South difference in overall publication and sequencing efforts (Fig. 4; Tables S3–S5).

The unbalanced geography of research effort, which is congruent among all studied marine and continental taxa within the Mediterranean Basin, is of utmost importance, as molecular barcoding is increasingly becoming the primary tool of analysis for taxonomists (e.g. see Yao et al., 2010 for plants and animals; Wu et al., 2019 for fungi). To avoid mapping more the sampling effort of researchers than the real diversity patterns of the studied taxa, and leaving behind vast areas which have been neglected in indexed publications and DNA-based initiatives, this uneven geography of knowledge should be taken into account when updating global biodiversity patterns.

6. Multi-taxa initiatives provide promising perspectives for a refined geography of biodiversity stakes

Since 2000, for every paper published in the Mediterranean, an average of 8.21 sequences have been deposited in public databases, covering an extremely wide range of both marine and continental taxa. DNA-based taxonomic knowledge induced changes in the delimitation of species, profound shifts in our understanding of the tree of life for both marine (e.g. sponges) and terrestrial (e.g. insects, fungi) organisms, and the emergence of a vast amount of taxonomic knowledge.

This molecular corpus awaits to be handled in multi-taxa analyses in order to improve our understanding of biodiversity patterns within the Mediterranean basin. This will certainly reveal contrasted conservation stakes between taxa across the hotspot, due to patterns of diversity and endemism that may not always be congruent. From an operational perspective, this will allow a better prioritisation of conservation efforts, and ensure that no areas of high conservation priority for hyper-diverse lineages are missed due to a low level of diversity or endemism of macro-organisms. To achieve this goal, the forthcoming initiatives may follow a three-step procedure.

- First, the unbalanced geographic distribution of biodiversity records within the hotspot highlights the need to implement multi-taxa metabarcoding initiatives in priority in the economically

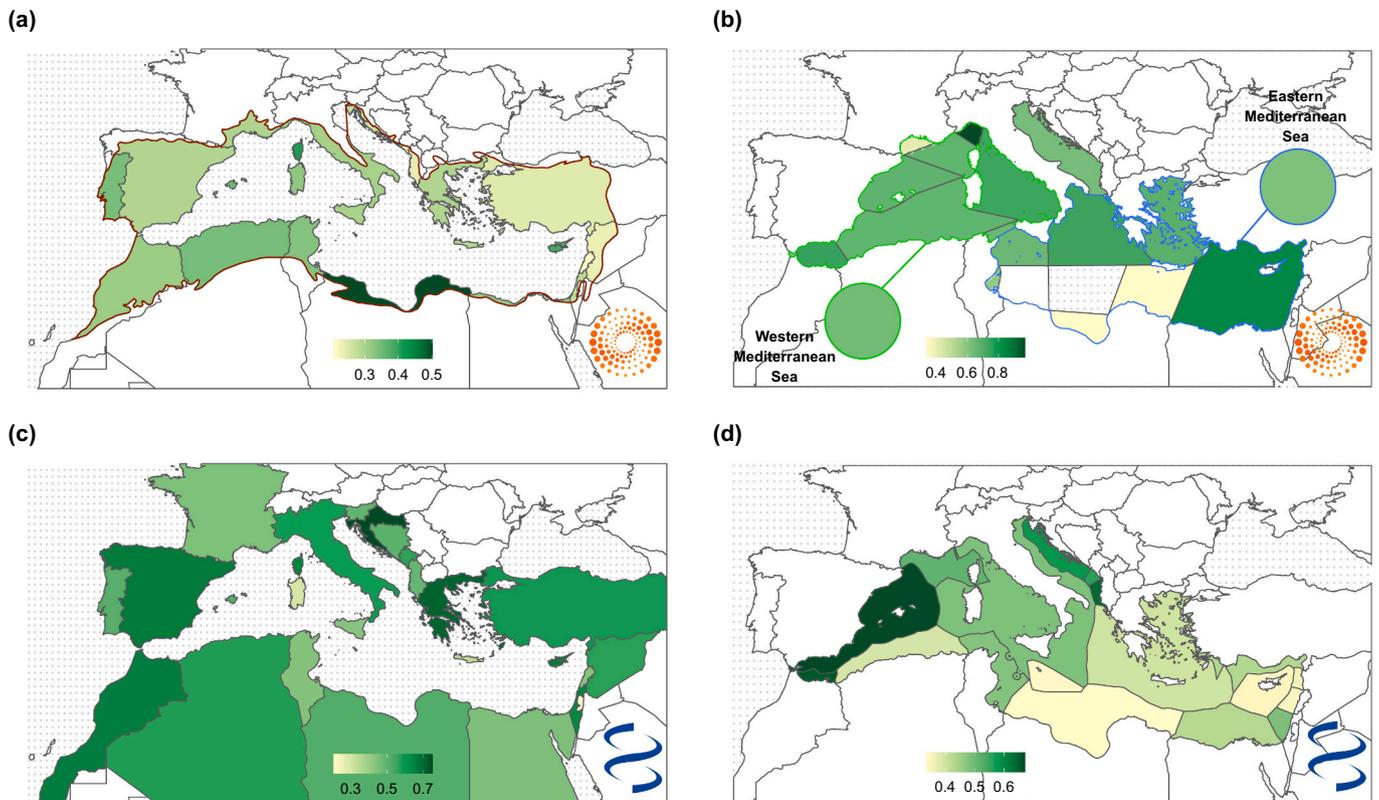


Fig. 4. Between-taxa evenness of the number of publications dealing with (a) continental and (b) marine taxa, and of the number of sequences deposited in GenBank for (c) continental and (d) marine taxa. The values are Simpson's evenness index, i.e. the closer the values are to 1, the more evenly distributed the number of publications or sequences are among the taxa, and the closer the values are to 0, the more a single taxa concentrates most publications or sequences.

disadvantaged parts of the hotspot (Fig. 2). These researches may benefit from the sharp decrease of sequencing costs during the last two decades and from the emergence of promising field-adapted technologies (e.g. Nanopore MinION Sequencing).

- Second, the highly contrasted ability of macro-organisms to shelter nested biodiversity supports the need for comparing distribution patterns of macro-organisms and hyper-diverse lineages throughout the Mediterranean basin. At this scale, mapping multi-taxa molecular data and biodiversity records may allow distinguishing between 1) high-priority sub-regions with congruently high conservation stakes for both kinds of organisms, 2) cold sub-hotspots with congruently low conservation stakes for both kinds of organisms and 3) contrasted areas, where macro-organisms and their associated biota show incongruent patterns of diversity or endemism. In addition to the previous network-based mechanism, we here predict that both evolutionary drivers and environmental filtering may have shaped a finer-scale mosaic of "global diversity sub-hotspots" within the Mediterranean basin, as previously evidenced for vascular plants (Médail and Baumel, 2018).
- Third, the millennial signature of Mediterranean societies combined its effects with environmental filtering, ecological and evolutionary processes to shape the current biodiversity patterns across the Mediterranean basin. As a consequence, adapted conservation strategies within sub-hotspots of global diversity should be designed in light of the balance between sociological and biological determinants. For instance, across the Iberian Peninsula, millions of hectares of Iberian Dehesas require the perpetuation of anthropogenic disturbances to maintain the patchy mosaic of habitats which conditions their high conservation value regarding macro-organisms, insects and fungi (Rodríguez-Rojo et al., 2022). Contrastingly, the exclusion of human practices within specifically designed areas certainly represents an appropriate response to the

highly valuable diversity sheltered by mountainous ecosystems dominated by endemic pine species (e.g. Thibault et al., 2006).

There is increasing evidence that long-term human legacies concern most ecosystems, including tropical forests which were until recently considered as relatively untouched by human activities (Grantham et al., 2020). As a consequence, the Mediterranean basin is a less singular region than previously thought, and may be used as a valuable research laboratory to develop guidelines for conservation strategies in most biodiversity hotspots.

CRediT authorship contribution statement

Jan Perret: Conceptualization, Project administration, Methodology, Software, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Océane Cobelli:** Conceptualization, Methodology, Software, Writing – review & editing. **Adrien Taudière:** Conceptualization, Methodology, Software, Writing – review & editing. **Julien Andrieu:** Writing – review & editing. **Yildiz Aumeeruddy-Thomas:** Conceptualization, Funding acquisition, Writing – review & editing. **Jamila Ben Souissi:** Writing – review & editing. **Guillaume Besnard:** Validation, Data curation, Writing – review & editing. **Gabriele Casazza:** Writing – review & editing. **Pierre-André Crochet:** Validation, Data curation, Writing – review & editing. **Thibaud Decaëns:** Validation, Data curation, Writing – review & editing. **Françoise Denis:** Writing – review & editing. **Philippe Geniez:** Validation, Data curation, Writing – review & editing. **Michael Loizides:** Writing – original draft, Writing – review & editing. **Frédéric Médail:** Validation, Data curation, Writing – review & editing. **Vanina Pasqualini:** Writing – review & editing. **Claudia Speciale:** Writing – review & editing. **Vincent Battesti:** Writing – review & editing. **Pierre Chevaldonné:** Methodology, Validation, Data curation, Writing –

original draft, Writing – review & editing. **Christophe Lejeune:** Methodology, Validation, Data curation, Writing – original draft, Writing – review & editing. **Franck Richard:** Conceptualization, Supervision, Methodology, Validation, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data and code used for this study are available from the GitHub repository: https://github.com/JanPerret/Biodivmex_git.

Acknowledgements

This study was funded by the program BioDivMeX (BioDiversity of the Mediterranean eXperiment), as a part of the metaprogram MIS-TRALS (Mediterranean Integrated STudies at Regional And Local Scales). We thank Jean-Michel Bellanger for his help with the molecular taxonomy of fungi.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110162>.

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