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Biodiversity hotspots: A shortcut for a more complicated concept

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ABSTRACT

In an era of human activities, global environmental changes, habitat loss and species extinction, conservation strategies are a crucial step toward minimizing biodiversity loss. For instance, oceans acidification and land use are intensifying in many places with negative and often irreversible consequences for biodiversity. Biodiversity hotspots, despite some criticism, have become a tool for setting conservation priorities and play an important role in decision-making for cost-effective strategies to preserve biodiversity in terrestrial and, to some extent, marine ecosystems. This area-based approach can be applied to any geographical scale and it is considered to be one of the best approaches for maintaining a large proportion of the world's biological diversity. However, delineating hotspots includes quantitative criteria along with subjective considerations and the risk is to neglect areas, such as coldspots, with other types of conservation value. Nowadays, it is widely acknowledged that biodiversity is much more than just the number of species in a region and a conservation strategy cannot be based merely on the number of taxa present in an ecosystem. Therefore, the idea that strongly emerges is the need to reconsider conservation priorities and to go toward an interdisciplinary approach through the creation of science-policy partnerships.

Contents

1. Introduction

As demonstrated by several researches, maintaining biodiversity is essential to the supply of ecosystem services and not less important to support their health and resilience (Pereira et al., 2013). However, despite there being an international interest to sustain and protect biodiversity, its loss does not seem to slow down (Butchart et al., 2010). Although there has been an extension of protected areas (Pimm et al., 2014), these provide a still low species coverage (Venter et al., 2014) and do not appear to optimally protect biodiversity (Pimm et al., 2014). For instance, a recent analysis (Selig et al., 2014) for conservation priorities in marine environments by combining spatial distribution data for nearly 12,500 species with human impacts information, identified new areas of high conservation value that are located in Arctic and Antarctic Oceans and beyond national jurisdictions.

Overall, habitat change and their over-exploitation, pollution, invasive species and in particular climate change are the major causes for biodiversity loss. The combined effect of these anthropogenic pressures may have already started a critical transition toward a tipping point (Barnosky et al., 2012). In particular, climate is modifying rapidly forcing biodiversity to adapt either through the change of habitat and life cycles or the development of new physical traits (Berteaux et al., 2010). For instance, rising temperatures can lead to potential biodiversity increases in northern regions (i.e. northern biodiversity paradox) where low temperatures usually are a limiting factor for the establishment of many species (Berteaux et al., 2010). Given the importance that biodiversity plays, the understanding of the main threats to biodiversity is today than ever before a central objective in conservation biology.

Nowadays there is serious concern about the effectiveness of existing strategies for biodiversity protection. A central issue in conservation is to identify biodiversity-rich areas to which conservation resources should be directed. Based on the observation that some parts of the world have far more species than others, the area-based approaches are widely advocated for species conservation planning. Areas with high concentrations of endemic species (species that are found nowhere else on Earth) and with high habitat loss are often referred to as "hotspots" (Myers, 1988). The hotspot approach can be applied at any geographical scale and both in terrestrial and marine environments. However, hotspots represent conservation priorities in terrestrial ecosystems but remain largely unexplored in marine habitats (Worm et al., 2003) where the amount of data is still poor (Mittermeier et al., 2011).

Despite this lack of homogeneity in data between terrestrial and aquatic ecosystems, the recent concerns over loss of biodiversity have led to calls for the preservation of hotspots as a priority. As reported by Myers (2003) at the end of his article, "Edward O. Wilson, one of the leading authorities on conservation, described the hotspot approach as '*the most important contribution to conservation biology of the last century*'". Closely linked to the concept of biodiversity, the hotspot concept is used with increasing frequency in biology and conservation literature and often with different meanings. While in a strict sense, the meaning is based on an estimate of endemic species and habitat loss, in a broad sense it refers to any area or region with exceptionally high biodiversity at the ecosystem, species and genetic levels.

The aim of this work is to review the current literature on the general concept of hotspots. We first introduce the approach that lies behind the concept of hotspots, in both terrestrial and marine ecosystems. Next we discuss the main criticisms and controversies concerning this approach and we present the possibility of using different alternative metrics to identify hotspots. Then we bring to light the links between biodiversity hotspots and marine pelagic ecosystem processes and we briefly introduce the deep-sea, a realm for the most part unknown for which several key questions are still waiting for an answer. Finally, we briefly discuss additional approaches and criteria, such as costs, in order to highlight some challenges in assigning global conservation priorities.

2. Biodiversity hotspots

2.1. The biodiversity hotspots concept

The British ecologist Norman Myers first published the biodiversity hotspot thesis in 1988. Myers, although without quantitative criteria but relying solely on the high levels of habitat loss and the presence of an extraordinary number of plant endemism, identified ten tropical forest "hotspots" (Mittermeier et al., 2011). A subsequent analysis (Myers, 1990) added a further eight hotspots, including four in Mediterranean regions. Conservation International (CI— http://www.conservation.org) adopted Myers' hotspots as its institutional blueprint in 1989, and afterwards worked with him in a first systematic update of the global hotspots. Myers, Conservation International, and collaborators later revised estimates of remaining primary habitat and defined the hotspots formally as biogeographic regions with >1500 endemic vascular plant species and ≤30% of original primary habitat (Myers et al., 2000). This collaboration, which led to an extensive global review (Mittermeier et al., 1999) and a scientific publication (Myers et al., 2000) saw the hotspots expand in area as well as in number, on the basis of both the better-defined criteria and new data. A second major revision and update in 2004 (Mittermeier et al., 2004) did not change the criteria but by redefining several hotspots boundaries, and by adding new ones that were suspected hotspots for which sufficient data either did not exist or were not easily accessible, brought the total to 34 biodiversity hotspots (Mittermeier et al., 2011). Recently, a 35th hotspot was added (Williams et al., 2011), the Forests of East Australia. The 35 biodiversity hotspots (Table 1, Fig. 1) that cover only 17.3% of the Earth's land surface are characterized by both exceptional biodiversity and considerable habitat loss (Myers et al., 2000). More precisely, hotspots maintain 77% of all endemic plant species, 43% of vertebrates (including 60% of threatened mammals and birds), and 80% of all threatened amphibians (Mittermeier et al., 2011; Williams et al., 2011).

Table 1

Biodiversity hotspots from 1988 to present.

Source: Modified from: Mittermeier et al. (2011).

Myers (1988)	Myers (1990)	Myers et al. (2000)	Mittermeier et al. (2004)	2011 Revision
Uplands of Western Amazonia	Uplands of Western Amazonia	Tropical Andes[a]	Tropical Andes	Tropical Andes
Western Ecuador	Western Ecuador			
Colombian Choco	Colombian Choco	Choco/Darien/western Ecuador[b]	Tumbes-Choco-Magdalena	Tumbes-Choco-Magdalena
Atlantic Coast Brazil	Atlantic Coast Brazil	Atlantic Coast Brazil	Atlantic Forest	Atlantic Forest
		Brazilian Cerrado	Cerrado	Cerrado
	Central Chile	Central Chile[a]	Chilean Winter Rainfall and Valdivian Forest	Chilean Winter Rainfall and Valdivian Forest
		Mesoamerica	Mesoamerica	Mesoamerica
			Madrean Pine-Oak Woodlands	Madrean Pine-Oak Woodlands
		Caribbean	Caribbean Islands	Caribbean Islands
	California Floristic Province	California Floristic Province	California Floristic Province	California Floristic Province
	Ivory Coast	Guinean Forest of West Africa[a]	Guinean Forest of West Africa	Guinean Forest of West Africa
	Cape Floristic Region	Cape Floristic Province	Cape Floristic Region	Cape Floristic Region
		Succulent Karoo	Succulent Karoo	Succulent Karoo
			Maputaland–Pondoland–Albany	Maputaland–Pondoland–Albany
	Tanzania	Eastern Arc and Coastal Forest of Tanzania/Kenya[c]	Eastern Afromontane[d]	Eastern Afromontane
			Coastal Forests of Eastern Africa[d]	Coastal Forests of Eastern Africa
			Horn of Africa	Horn of Africa
Eastern Madagascar	Eastern Madagascar	Madagascar and Indian Ocean Islands	Madagascar and Indian Ocean Islands	Madagascar and Indian Ocean Islands
		Mediterranean Basin	Mediterranean Basin	Mediterranean Basin
		Caucasus	Caucasus	Caucasus
			Irano-Anatolian	Irano-Anatolian
			Mountains of Central Asia	Mountains of Central Asia
	Western Ghats in India			
	Southwestern Sri Lanka	Western Ghats and Sri Lanka[b]	Western Ghats and Sri Lanka	Western Ghats and Sri Lanka
		Mountains of South-Central China	Mountains of South-Central China	Mountains of South-Central China
			Indo-Burma	Indo-Burma
Eastern Himalayas	Eastern Himalayas	Indo-Burma[e]	Himalaya[f]	Himalaya
Peninsular Malaysia	Peninsular Malaysia			
Northern Borneo	Northern Borneo	Sundaland[b]	Sundaland	Sundaland
		Wallacea	Wallacea	Wallacea
Philippines	Philippines	Philippines	Philippines	Philippines
			Japan	Japan
	Southwest Australia	Southwest Australia[a]	Southwest Australia	Southwest Australia
				Forests of East Australia[g]
			East Melanesian Islands	East Melanesian Islands
		New Zeeland	New Zeeland	New Zeeland
New Caledonia	New Caledonia	New Caledonia	New Caledonia	New Caledonia
		Polynesia–Micronesia	Polynesia–Micronesia	Polynesia–Micronesia

[a] Expanded.

[b] Merged and/or expanded.

[c] Expanded to include Coastal Forests of Tanzania and parts of Kenya.

[d] The Eastern Arc and Coastal Forests of Tanzania/Kenya hotspots was split into the Eastern Afromontane hotspot (the Eastern Arc Mountains and Southern Rift, the Albertine Rift, and the Ethiopian Highlands) and Coastal Forests of Eastern Africa (southern Somalia south through Kenya, Tanzania and Mozambique).

[e] Eastern Himalayas was divided into Mountains of South-Central China and Indo-Burma, the latter of which was expanded.

[f] The Indo-Burma hotspot was redefined and the Himalayan chain was separated as a new Himalayan hotspot, which was expanded.

[g] The Forests of Eastern Australia the 35th biodiversity hotspot.

Biodiversity is important in the oceans as on land. Myers and colleagues, however, excluded the oceans from their analysis. In particular, coral reefs are one of the most biologically diverse ecosystems in the ocean and provide important structures and habitat in tropical and sub-tropical coastal waters (Bellwood et al., 2004). In these areas, where the explanation for the high number of species is still debated (Bowen et al., 2013; Cowman et al., 2013), ocean acidification and changes in sea surface temperature (Ateweberhan et al., 2013) are likely to cause major coral reef losses and changes in the distribution and
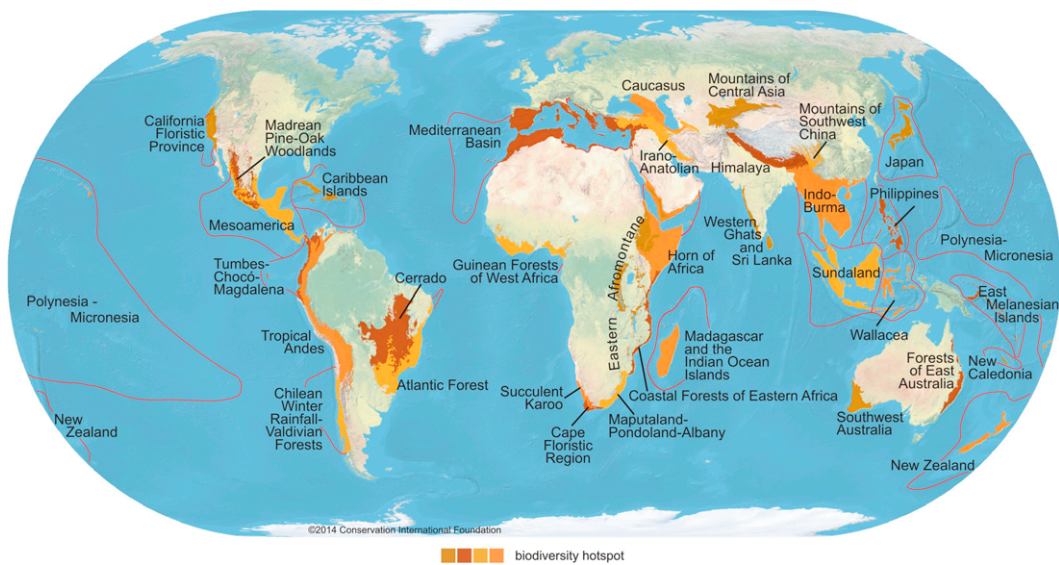
Fig. 1. The world's biodiversity hotspots (see also Table 1 for hotspots names). Figure licensed under the Creative Commons Attribution-Share Alike 4.0 International license (Author: Conservation International).

relative abundances of marine organisms. Moreover, apart from the intrinsic biodiversity value, there are economic arguments for the protection of marine biodiversity (Balmford et al., 2002). This makes the maintenance of marine biodiversity a valuable environmental management goal. Roberts et al. (2002), through the publication of one of the most comprehensive studies of hotspots on global coral reefs, have brought much-needed attention to marine hotspots, extending the hotspot concept to coral reefs and arguing that biodiversity hotspots are major centers of endemism in the sea as well as on land. Overall, the analysis revealed the 18 richest multi-taxon centers of endemism, of which 10 were considered to be marine biodiversity hotspots. Furthermore, 8 of 10 marine biodiversity hotspots and 14 of 18 centers of endemism were found to be adjacent to terrestrial biodiversity hotspots, suggesting a possible integration among terrestrial and marine conservation (Roberts et al., 2002).

2.2. Criticism of biodiversity hotspots

Since its introduction, the concept of hotspots was used as a key strategy for global conservation action. For this reason, it has become the principal global conservation-prioritization approach, attracting over $1 billion in conservation investment (Sloan et al., 2014). The approach is thus partly economic and it is based on the fact that it is not possible to protect the full range of biodiversity since it would certainly not be a realistic target. Basically, biodiversity conservation requires prioritization to be effective, if only because funds are limited and must be allocated carefully (Myers, 2003). Therefore, among many others, entities like Conservation International, have explicitly adopted the hotspot concept as a central conservation-investment strategy (Sloan et al., 2014).

In a 2003 essay entitled "Conserving Biodiversity Coldspots", conservation biologists Peter Kareiva and Michelle Marvier argued that non-governmental organizations, foundations and international agencies have been seduced by the simplicity of the hotspot idea, and significant financial resources (Dalton, 2000) have been directed toward them. In particular, the two conservation biologists argued that coldspots, despite begin poorer for number of species, play an important ecological role. By investing exclusively in hotspots and ignoring coldspots the risk is to lose large, natural and ecologically important areas that contribute to many ecosystem services (Kareiva and Marvier, 2003). On the same wavelength, Jepson and Canney (2001) have warned that the biodiversity hotspots approach provides only a partial response for the conservation. The authors agree that promoting biodiversity hotspots, as a "silver bullet" strategy for conserving the most species for the least cost is a risk in complex areas of international policy, such as biodiversity conservation, because decision makers may view it as a cure-all. As a result, they conclude that spatial priorities and public policy cannot be determined on the basis of simple species counts, which is the foundation of the biodiversity hotspot approach. Furthermore, as pointed out by Smith et al. (2001) biodiversity hotspots entirely ignore regions of ecological transition. Hence, the authors promote a more comprehensive approach to include regions important to the generation and maintenance of biodiversity, regardless of whether they are "species-rich". Recently, Stork et al. (2014) have emphasized the lack of consideration for the role of invertebrates (e.g. herbivorous insects, herbivorous fungi and nematodes) in decision-making about global biodiversity hotspots, suggesting a more detailed analysis of the role of plants as umbrella species for these herbivorous organisms.

Furthermore, since data on species distributions are usually scarce the conservation of an entire global hotspot may be difficult and unsustainable. In this regard, Cañadas et al. (2014) pointed out the need to focus strategies on small areas that represent maximum diversity and/or endemism. Finally, for some of the same reasons that fueled disputes for terrestrial ecosystems, hotspots on coral reefs (Roberts et al., 2002) have also been the subject of controversy (Briggs, 2002; Hughes et al., 2002). In this respect, Parravicini et al. (2014) have recently identified tropical reef areas that are critical for preventing the loss of fish taxonomic and functional biodiversity. These areas, such as the Western Indian Ocean, differ in important ways from the fish richness hotspots previously identified close to the Indo-Australian Archipelago.

These criticisms highlight the problems associated with the idea of biodiversity hotspots, even though Myers (2003) (whose criteria include endemism and species richness) points out that other criteria are not ruled out by the theory itself. Essentially, the author affirms that the hotspot approach does not exclude other areas that need conservation, but nevertheless claims that a conservation strategy will always need a measure to determine priorities. In conclusion, although not completely free from criticism, the hotspot approach has become a key tool to guide conservation efforts and presently plays a leading role in decision-making regarding conservation cost-effective strategies (O'Donnell et al., 2012).

3. Hotspots identification

Biodiversity hotspots are particular areas where extraordinary concentrations of biodiversity exist. Although hotspots have also been identified through different ways (Hoekstra et al., 2005), these areas are usually defined by one or more species-based metrics (number of species – species richness; number of species restricted to a particular area – endemic-species richness; and number of rare or threatened species) or focusing on phylogenetic and functional diversity in order to protect species that support unique and irreplaceable roles within the ecosystem.

3.1. Species-based metrics

A central issue in conservation today is to identify biodiversity-rich areas. Species richness (SR) has been the main focus of conservation studies and is still widely used, mainly because it is easy to quantify and interpret data (Davies and Cadotte, 2011). In particular, conservation planning has traditionally used richness information combined with different irreplaceability measures (e.g. endemism or rarity) to prioritize some regions over others (e.g. biodiversity hotspots). In the methodology proposed by Myers et al. (2000), the key factors considered for the analysis were: (1) numbers of endemics and endemic species/area ratios for both plants and vertebrates, and (2) habitat loss. More precisely, vascular plants were chosen as the metric for endemism because fairly well known and essential to all forms of animal life, while vertebrates (four groups: mammals, birds, reptiles and amphibians) were mainly used to determine congruence and to facilitate other comparisons among the hotspots. However, the analysis omitted invertebrates because they are not yet well documented and fish, because of lack of good data. Finally, the boundaries of the hotspots were determined by examining biological commonalities with each of the areas featuring a separate biota or community of species that fits together as a biogeographic unit. Therefore, selecting biodiversity hotspots requires data on species distributions together with the definition of a threshold useful to define the boundaries between hotspots and non-hotspots (Cañadas et al., 2014).

Increasing evidence, both in marine and terrestrial environments, shows that hotspots of total species richness are not always concordant with hotspots of endemism or threat. Concentrations of threatened species or local endemics may also occur in areas of lower richness (Hughes et al., 2002). Orme et al. (2005), using a global database to map the geographical distribution of birds, found an alarming lack of congruence between hotspots defined with the criterion of species endemism and areas of high species richness and concentrated threat. Furthermore, species richness for one taxon may not match perfectly with hotspots in the richness of another (Davies and Cadotte, 2011). For example, while Lamoreux et al. (2006) have found high congruence between conservation priorities for terrestrial vertebrate species, Grenyer et al. (2006) reported low congruence between conservation priorities for mammals, birds, and amphibians. Recently, a new assessment of global conservation priorities (Jenkins et al., 2013) mapped global priority areas using the latest data on mammals, amphibians, and birds at a scale 100 times finer than previous assessments (Ceballos and Ehrlich, 2006; Grenyer et al., 2006; Lamoreux et al., 2006). This analysis has identified areas in the world that are currently ignored by biodiversity hotspots but critical for preventing vertebrate extinctions. Finally, focusing on small areas Cañadas et al. (2014) showed that even in areas that are noted to be hotspots, the endemic-plant richness is not uniformly distributed, but rather depends largely on environmental conditions. Specifically, according to the authors, it is possible to identify hotspots within hotspots that can be organized in a hierarchy helping to focus conservation efforts at different scales within a given hotspot.

3.2. Phylogenetic diversity

The use of species-based metrics remains the primary method for characterizing and mapping the distribution of biological diversity and thus to identify areas as biodiversity hotspots. However, because diversity, or evolutionary history, is distributed unequally between taxa as well as between areas, taking into consideration only traditional species diversity may not be sufficient to fully capture differences among species (Chao et al., 2014). Therefore, to quantify biodiversity the focus shifted from pure species counting to a more integrative approach that quantifies the evolutionary information represented within groups of taxa (i.e. phylogenetic diversity, PD) along with the diversity of ecological traits (i.e. functional

diversity, FD). The loss of FD or PD per unit of habitat loss may be a better indicator of ecosystem vulnerability, providing a more comprehensive measure than those based exclusively on the loss of single species. Recently, D'Agata et al. (2014) showed that despite a minimal loss of fish richness that can occur along a human pressure gradient, many functions and phylogenetic lineages might be lost. PD might thus be more useful than species richness in maintaining ecosystem services (Cadotte and Davies, 2010). Its use redefines the identification of species of conservation interest by taking into consideration the evolutionary information represented within groups of taxa, providing additional information to guide conservation decision-making. Phylogenetic information is increasingly being used in ecological studies (Cadotte et al., 2010) in parallel with an increasing number of new and sophisticated metrics that incorporate different community attributes such as abundance information and geographical rarity (Cadotte and Davies, 2010; Cadotte et al., 2010). Probably, the increasing availability of molecular data and the recent advances in software and phylogenetic methods (Roquet et al., 2013) will enhance even more the use of phylogenetic information to better characterize and describe biodiversity patterns and ecosystem functioning.

3.3. Which metric?

A limiting factor in conservation assessments is the availability of appropriate and quality data on spatial information upon which the effectiveness of conservation planning depends. For example, assessing endemism in the western Amazon (one of the world's last high-biodiversity wilderness areas) continues to be a major challenge and vast areas have yet to be surveyed by scientists, and in consequence many species distributions are poorly known (Bass et al., 2010). Moreover, biodiversity is not an easy concept to measure and the choice of metrics to define hotspots is thus an important and sensitive issue that may lead to different conclusions regarding the future positioning of hotspots (Possingham and Wilson, 2005). For instance, a recent study (Stuart-Smith et al., 2013) by integrating abundance and functional traits revealed new global hotspots of fish diversity and identified unrecognized biodiversity value in some temperate and southern hemisphere marine regions.

Species richness has been a convenient criterion to identify hotspots (Cadotte and Davies, 2010). However, as noted above, biodiversity metrics might better reflect spatial diversity patterns for biogeography and conservation planning by considering evolutionary history and functional diversity. Although measures of species richness assume all species have equal weights, a common criticism of the alternative diversity metrics is that they are sensitive to the calculations and the weighting scheme used to construct them (Tucker et al., 2012). As evidenced by Cadotte and Davies (2010), the reliability of these metrics is closely linked with the quality of the underlying phylogenetic and distributional data. The choice of a particular metric can, therefore, significantly alter conservation priority. Recently, understanding if there is a broad agreement between the results obtained from the use of different metrics has become of common interest to correctly detect biodiversity distribution patterns and identify diversity hotspots. For instance, Mazel et al. (2014) have found that SR, PD and FD are not necessarily good surrogates for each other. Furthermore, the effect of considering PD metrics in existing conservation planning is still debated (Rosauer and Mooers, 2013; Winter et al., 2013). Recently, Zupan et al. (2014) investigated patterns of PD in relation to species diversity across three european taxonomic groups (birds, mammals and amphibians) to evaluate their congruence and to emphasize areas of particular evolutionary history. Results indicated that phylogenetic diversity patterns strongly mismatch in space between groups and demonstrated that the diversity of one taxonomic group is not representative of the diversity of other groups. Very likely, the increasing availability of phylogenetic data and advances in informatics tools may continue to facilitate a rapid expansion of studies that apply PD metrics and methods to community ecology (Cavender-Bares et al., 2009). Finally, the development of ever more sophisticated metrics (Rosauer et al., 2009; Cadotte et al., 2010) may help to provide new and significant information into the mechanisms that underlie the current patterns of biological diversity across different spatial scales.

Focusing our attention once again on species-based metrics, it is possible to consider the conservation status, which indicates the probability that a given species is vulnerable, at risk or close to extinction. For example, the IUCN Red List of Threatened Species (http://www.iucnredlist.org/) was conceived for this purpose becoming through time the most used system for assigning species' threat status (Keith et al., 2014). Nowadays the IUCN Red List may be used to aid effective conservation strategies by incorporating genetic data (Rivers et al., 2014), in conjunction with models to detect extinction risk from climate change (Keith et al., 2014) and to identify species at extinction risk using global models of anthropogenic impact (Peters et al., 2014).

Finally, terrestrial biodiversity can be modeled at different scales using remote sensing. Remote sensing is a useful tool to orient fieldwork, predict spatial patterns and to improve species richness models (Camathias et al., 2013). Especially, remote sensing can greatly aid conservation decisions, which are often made with relatively sparse information (Pressey, 2004) providing high-resolution spatial data and continuously updated information on habitat status (area and degradation), alterations in species diversity and distribution, and trends in pressures and threats. As summarized in a recent review (Nagendra et al., 2013), different studies have used remote sensing tools and satellite imagery to quantifying terrestrial biodiversity (e.g., Hernández-Stefanoni et al., 2012 and Mazor et al., 2013). Remote sensing shows thus great promise for monitoring, managing protected areas and protecting biodiversity (see also Pettorelli et al., 2014 for an up-to-date review). Basically, at this point, the improvement of existing technologies together with a better availability of global data quality on species ecologies and geographies represent an opportunity to improve our understanding on biodiversity patterns and to make a difference in environmental management.

4. Marine hotspots

Oceanic ecosystems sustain the human well being by providing major services like jobs and food supply. Due to climate change, physical and chemical conditions marine ecosystems are changing with time (Doney et al., 2012). In particular, ocean acidification represents a major threat to biodiversity (Sunday et al., 2014) whose maintenance promotes ocean health and service provision (Worm et al., 2006). Overall, the marine environment comprises two distinct and interconnected realms. The entire area of the open water is the pelagic realm and the pelagic organisms are those that live in the open sea away from the bottom. This is in contrast to the benthic realm, which is a general term referring to organisms and zones of the sea bottom. Oceanic waters and the deep-sea are here defined as waters and sea-floor areas over 200 m of depth.

4.1. Pelagic hotspots

The identification and monitoring of pelagic hotspots in marine ecosystems could constitute an effective approach to ocean conservation and resource management. However, the hotspot concept that fits well to more "static" marine habitats such as coral reefs (Roberts et al., 2002) is more difficult to apply in pelagic ecosystems (oceanic waters) where both boundaries and features are in constant movement due to the presence of highly dynamic physical processes (Hazen et al., 2013). For instance, this aspect is particularly evident in Arctic Ocean where oceanic fronts, polynyas or marginal ice zone, act as local hotspots of both productivity and biodiversity. In this dynamic context, it is thus important to examine biotic and abiotic environmental predictors (e.g. bathymetry, shelf-breaks, sea surface temperature, chlorophyll-a) of hotspots occurrence in order to explain their spatial distribution and persistence. As a consequence, the hotspot concept applied to marine ecosystems has received somewhat mixed definitions (e.g., Worm et al., 2003; Piatt et al., 2006 and Sydeman et al., 2006). Overall, hotspots in the epipelagic zone have been described as areas where, relatively to the surrounding environment, particular and favorable physical condition promote high biological activity and thus the aggregation of primary and secondary consumers (Palacios et al., 2006). In these areas, upwelling, mesoscale eddies, and fronts may act in accordance with the local geomorphology to generate conditions that greatly promote the availability of prey for large fauna (Wingfield et al., 2011; Sigler et al., 2012). For example, seamounts are fixed locations but can act as biodiversity hotspots, attracting top pelagic predators and migratory species (Morato et al., 2010). Fundamentally, physical processes leading to hotspot formation and persistence are different and operate through different spatial and temporal scales. Mesoscale structure (10–1000 km; days to months) can determine the occurrence and persistence of marine hotspots and provide criteria for defining areas of high trophic transfer (Hazen et al., 2013). For example, cyclonic eddies enhancing nutrient inputs to the surface ocean are important sources of biological production that may contain high concentrations of biomass and probably affect the spatial and temporal variation in top predator hotspots (Santora and Veit, 2013).

Finally, given the dynamic nature of pelagic hotspots the integration of shipboard based studies with satellite remote sensing data may help to resolve possible spatio-temporal mismatches (Hazen et al., 2013). Although limited to surface conditions, due to their ability to sample local to global spatial scales over days to years, satellite-based observations of ocean conditions offer the greatest opportunity to quantify the persistence of many marine hotspots in space and time (Palacios et al., 2006). The primary biological indicator accessible remotely from space is the phytoplankton chlorophyll-a concentration, a good proxy of ocean productivity, which in turn has a significant effect on marine biodiversity (Corliss et al., 2009). For instance, Suryan et al. (2012) used a satellite-derived peak of surface chlorophyll-a as an index to identify seabird hotspots. Recently, a variety of bio-optical and ecological methods (Brewin et al., 2014) have been established to use satellite data to identify and differentiate between phytoplankton functional types (PFTs) that are relevant proxies of ecosystem functioning. The attempts to identify PFTs from space represent a new frontier, which no doubt has potential for further improvement. Remote sensing of ocean color, besides being an established tool to observe the global distribution of phytoplankton, may thus contain untapped potential for marine biodiversity studies. However, it is just as important to realize that remote sensing cannot provide all the answers. Recently, to provide support for the assessment of the state of the marine ecosystem, Racault et al. (2014) proposed a suite of plankton indicators from different observing systems (e.g. mooring stations, ships, autonomous floats and remote sensing) and subsequently have classified them in an ecological framework that characterizes key attributes of the marine ecosystem. Finally, remote sensing analysis can be used in fisheries management (Chassot et al., 2011) and to characterize marine protected areas (Kachelriess et al., 2014) based on the dynamics of oceanographic boundaries (and thus in areas beyond national jurisdiction which remain vulnerable to uncontrolled exploitation) rather than on geographic boundaries employed by traditional marine protected areas. As long-term time series become available in the near future, remote sensing will offer opportunities to identify resilient pelagic marine hotspots.

4.2. Deep-water hotspots

Deep-sea ecosystems, which include the waters and sediments beneath approximately 200 m depth covering more than 65% of the Earth's (Danovaro et al., 2010) are going toward widespread changes in benthic ecosystems and the functions and services they provide (Jones et al., 2014). In particular, biodiversity hotspots such as seamounts, canyons, and cold-water coral reefs (Ramirez-Llodra et al., 2010), may be projected to experience changes in benthic food supply (Jones et al., 2014)

with a significant impact on the distribution of species richness (Gambi et al., 2014). However, because of the vastness and remoteness of the habitats (the majority of which are found in international waters) the management and conservation of deep-sea ecosystems is not an easy task (Ramirez-Llodra et al., 2010) and several key questions are still waiting for an answer. Only recently deep-sea biodiversity was incorporated in the analysis of global biodiversity through international monitoring programs (Weaver et al., 2004; Brandt et al., 2014), the outcomes of which might contradict the assumptions and paradigms advanced in the past (Danovaro et al., 2014). For instance, recent results showed the existence of an exponential relationship between ecosystem functioning and deep benthic biodiversity (Danovaro et al., 2008). These new observations suggest that (1) open continental slope systems and deep basins are characterized by positive functional interactions between different seafloor organisms and (2) indicate that a considerable biodiversity loss in deep-sea ecosystems might be lead to a drastic abatement of the key ecosystem processes (Danovaro et al., 2008, 2009). However, the two major trends in deep-sea biodiversity, the latitudinal and bathymetric gradients, are still strongly debated.

Preliminary results based on a large dataset collected during a collaborative project have provided new insights into latitudinal patterns (Danovaro et al., 2009) but their existence in deep-sea habitats remains still debated (Berke et al., 2014). For instance, while findings suggest that deep-sea diversity in the Southern Ocean presents high levels of biodiversity (Brandt et al., 2014) in the Northern Hemisphere studies with larger and more robust datasets are required to fill data gaps. In the Arctic, apart from works that have investigated the distribution and diversity of benthic fauna in specific areas of the Arctic sea (Meyer et al., 2014), not many studies have been carried out to explicitly investigate the relationship between biodiversity and ecosystem functions (Link et al., 2013). However, a recent review that has achieved an inventory of benthic diversity of pan-Arctic shelves (Piepenburg et al., 2011), seems to confute the common paradigm of low Arctic diversity, providing evidence that Arctic shelves are not particularly impoverished.

About the bathymetric gradient, qualitative and quantitative sampling studies indicated a relationship between diversity and depth with a peak at mid-slope depths (Ramirez-Llodra et al., 2010). However, although some hypotheses together with biological and environmental factors have been proposed to explain why species diversity changes as a function of depth, the mechanisms that potentially control bathymetric patterns have not yet been fully understood (Danovaro et al., 2009). For instance, some abyssal regions (e.g. the Equatorial Pacific and Southern Ocean) are characterized by very high diversity (Ramirez-Llodra et al., 2010). The rate, nature and spatial variability of food supply can play a key role in modulating ecosystem structure and function (Smith et al., 2008). Recently, a long time series data was used to document the importance of large episodic pulses of particulate organic carbon (POC) as vital food supply for abyssal communities (Smith et al., 2014). The analysis of time series reveals that in the past few years these pulses have increased in magnitude. Such increases in food supply that appears to change the structure and functioning of deep-sea communities seem to be connected with changes in surface ocean conditions (Smith et al., 2013). These outcomes suggest that different taxa may display different spatial patterns with increasing depth and thus, as evidenced by other authors (Ramirez-Llodra et al., 2010), the hump-shaped curve (Weaver et al., 2004) does not represent the general rule. Certainly, topographic and geological features may also play a key role in shaping the biodiversity spatial patterns (Danovaro et al., 2009). For instance, seamounts can act as biodiversity hotspots, attracting top pelagic predators and migratory species, such as whales, sharks, tuna or rays (Morato et al., 2010), as well as hosting a seafloor fauna with a large number of endemic species (Stocks and Hart, 2007). Considering the particularity and importance of these particular areas (Clark et al., 2010) a new method that uses seamounts has been recently proposed (Clark et al., 2014) for the selection of candidate "Ecologically or Biologically Significant Marine Areas" (EBSAs). Certainly the development of new methods, international monitoring programs and new technologies can promote, as advocated by some organizations such as Convention on Biological Diversity (CBD), the conservation of open-ocean and deep-sea ecosystems.

5. Biodiversity conservation and priorities

Biodiversity conservation, for several reasons (e.g. climate change), cannot be considered an easy task and the establishment of priorities therein is complex. Given this intrinsic difficulty, developing a global biodiversity observation system might look something insurmountable (Pereira et al., 2013). However, a growing number of environmental organizations together with the scientific community are working on a number of different approaches (Table 2) to identify biodiversity patterns, threats and locations for future acquisition or management. (Schmitt, 2011). These approaches, which prioritize globally important areas for biodiversity conservation, are based on two key ecological selection criteria (vulnerability and irreplaceability) and can be grouped into three main categories: proactive, reactive and representative (Schmitt, 2011). Like the hotspot approach, these efforts usually depend on species as the relevant unit of biodiversity, some important biodiversity dimensions, such as genetic diversity is often lacking (Pereira et al., 2013) and none of these approaches directly incorporate economic costs (Brooks et al., 2006). However, although their importance is still debated (Duke et al., 2013), economic costs could represent an important step in conservation planning. For instance, a recent study (Venter et al., 2014) clearly demonstrates that considerable increase in global protected area coverage of species could be achieved at minimal additional cost with a consequent improvement in biodiversity trends (Butchart et al., 2012). Incorporating information on costs and biodiversity benefit could thus provide a more cost-efficient allocation of limited conservation resources. In this respect, results from a recent study (Waldron et al., 2013) showed that funding for conservation measures is scarce despite the high levels of threatened biodiversity. Finally, as evidenced by Duffy et al. (2013), there is not a proactive marine biodiversity observation network for monitoring and evaluating global ocean biodiversity.

Table 2
The proactive, reactive and representative approaches used for the selection of biodiversity conservation priority areas at global scale. All the approaches are based on a combination of the ecological criteria of vulnerability and irreplaceability.
Source: Modified from: Schmitt (2011).

Approach	Organization	Vulnerability	Irreplaceability
Proactive approaches			
Frontier forests	World Resources Institute	Low	Low
Last intact forest landscapes	Greenpeace	Low	Low
Last of the wild	Wildlife Conservation Society	Low	Low
Wilderness areas	Conservation International	Low	Low
High biodiversity wilderness	Conservation International	Low	High
Reactive approaches			
Biodiversity hotspots	Conservation International	High	High
Alliance for Zero Extinction (AZE)[a]	52 Conservation organizations	High	High
Key biodiversity areas (KBAs)[a]	Conservation International Birdlife International Plantlife International	High	High
Important Bird Areas (IBAs)[a]	Birdlife International	High	High
Representative approaches			
Centers of plant diversity	WWF/IUCN		High
Endemic Bird Areas (EBAs)	Birdlife International		High
Global 200	WWF		High
Megadiversity countries	Conservation International		High

[a] Site-specific approaches.

Another issue is the loss of habitat structure that generally leads to a decline in species richness and biomass. The combined impacts of climate change and land use are expected to drive unprecedented rates of environmental change and biodiversity loss (Riordan and Rundel, 2014). In particular, climate change is likely to have a large impact on biodiversity, from organisms to biomes (see Bellard et al., 2012 for a exhaustive review). In this respect, recent studies (Bellard et al., 2014a,b) examined the potential effects of global changes on hotspots. Results showed that 19% of the insular biodiversity hotspots might be entirely submerged by the global sea level rise while, by a combined effects of global changes, hotspots might experience an average loss of 31% of their area, with some hotspots more affected than others (e.g. Polynesia–Micronesia). Approaches that integrate climate change adaptation into conservation planning (see Watson et al., 2012 for a review) are vital to monitor biodiversity responses and thus to maintaining the resilience of hotspots (Bellard et al., 2014b).

Finally, other dimensions of the problem, such as ecosystem services, need to be considered as well. Basically, changes in biodiversity can influence ecosystem processes and an alteration of these can influence ecosystem services (Diaz et al., 2006). Although there is still disagreement in the scientific community (Reyers et al., 2012; Schröter et al., 2014), ecosystem services-based strategies could be used for specific conservation actions (Bhagabati et al., 2014) and for protected areas designation (Potts et al., 2014). Anyhow, the exploration of possible congruencies between the targets of protecting ecosystem services and conserving biodiversity (Turner et al., 2007) is still difficult. The absence of credible, reproducible and sustainable frameworks makes the integration of ecosystem services into decision making still debated (Daily et al., 2009).

6. Conclusion

In 1988, Norman Myers published the first of a series of high-impact articles on global biodiversity hotspots that opened the way for a new strategy of nature conservation. Although not entirely free from criticism, the hotspot approach has played an important role in conservation prioritization. Since it is not possible to conserve all biodiversity due to lack of resources, international conservation agencies have used it as the most effective approach to minimize species extinctions on a global scale. However, focusing all the conservation attention on biodiversity hotspots could create a disproportionate impact on the maintenance of biodiversity in other biomes. For instance, although desert ecosystems cover 17% of the world's landmass and harbor surprisingly high biodiversity, they have not received substantial financial support for conservation actions (Durant et al., 2014). An optimal conservation network would then include both areas with high levels of diversity, as well as larger coldspots that are home to rare species (Kareiva and Marvier, 2003). Not surprisingly, recent results (Mouillot et al., 2013) emphasize the importance of rare species conservation and a more detailed understanding of the role of rarity and functional vulnerability in ecosystem functioning. Basically, coldspots could be as good as hotspots for directing conservation strategies since they might provide important ecosystem services. As pointed out by Bøhn and Amundsen (2004), an interesting study (Price, 2002) showed that stressful marine environments with low species richness could unexpectedly be both hotspots and coldspots of biodiversity. This may seems unusual, but as mentioned by the authors it represents a lack of focus on the ecological processes and interaction between organisms. Essentially, with the loss of the diversity of interactions and processes within and between organisms, the major risk is to irreversibly disrupt the integrity of the ecosystems and consequently the possibility to preserve functions and evolutionary processes indispensable to the maintenance and creation of new life (Bøhn and Amundsen, 2004).

Furthermore, another dimension of the problem, such as the incongruence among diversity metrics, needs to be considered as well. The identification of biodiversity hotspots frequently relies on the basis of partial knowledge and is commonly

based on an assumption that areas significant for well-known species are also important for other species. This implies that measures of diversity in different groups of organisms are highly correlated, but as we have seen, it may not always be necessarily true. Nonetheless, as previously reported, the development of new metrics that consider multiple aspects of biodiversity could help to provide new insights into the mechanisms that underlie the current patterns of biological diversity. Nowadays, an increasing number of studies (e.g., Daru et al., 2014) reinforce the need to adopt more integrative strategies, which considering evolutionary components and geographical distribution data, can better identify areas of high conservation priority.

Finally, it is becoming clear that the biodiversity hotspots approach represents a shortcut for a more complicated concept that is part of a bigger picture that includes consideration of ecosystem services, policies, costs, social preferences, and other factors, such as human activities and climate change. As mentioned by several authors, we need to go toward a common, modern and broader vision of biodiversity conservation. Scientific community, together with decision-makers in agencies, governments and non-governmental organizations, should thus carefully reconsider conservation priorities and, possibly, in order to avoid duplicating efforts (Mace, 2000), establish close partnerships (Berteaux et al., 2010; Maury et al., 2013) to develop successful conservation strategies for biodiversity management (Heller and Zavaleta, 2009). Because of the complexity of the topic and the unpredictability brought by climate change, there is no single definitive praxis to effective conservation, but rather an interdisciplinary approach. (Pohl and Hadorn, 2008) that is necessary today as never before.

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