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CHALLENGE 3

ABSTRACT

In the twenty-first century, biodiversity erosion has become a key scientific question at the time societal concern has increased. We propose theoretical, technological and policy-relevant challenges to preserve biodiversity and safeguard our options for future solutions to global environmental problems. We outline research areas to uncover naturally occurring processes, and to predict and mitigate the impact of global change.

KEYWORDS

ecosystem services environmental policies human-wildlife conflicts invasive species microbial communities

next-generation monitoring

CHALLENGE 3

PRESERVING BIODIVERSITY AND ITS FUNCTIONS UNDER GLOBAL CHANGE

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1. INTRODUCTION AND GENERAL DESCRIPTION

Biodiversity is threatened worldwide by human-induced rapid environmental changes in climate and land- / sea-use, pollution, and biotic exchange, i.e. by stressors ultimately linked to the rise of global human population and the advance of economic development (Chapin et al. 2000). The recent global assessment of the Intergovernmental Science- Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019) warns that one million animal and plant species are threatened, alien species doubled in the last 50 years, and wild populations have lost about 1% of their genetic diversity per decade in the last 150 years. Moreover, 40 % of the world's land has been converted to agricultural or urban land and 87 % of the ocean has been to some extent altered. This means that biological diversity is eroded at all its levels, from the genetic variability of populations to the diversity of species and the ecosystems in which they live, a loss that ultimately compromises the functioning of ecosystems and their ability to provide services to humans (Loreau et al. 2001).

Although biodiversity should be protected for its own sake to maintain a healthy planet, and for the sake of humans for our own well-being, its preservation is often perceived as a trade-off with other competing interests such as human development or resource production. Delineating win-win approaches that balance conservation and human activities is difficult and complicate the optimization of conservation strategies. A single target similar to, e.g., climate-change objective of not reaching a global 1.5 °C increase in temperature above pre-industrial levels (Paris Agreement Report http://go.nature. com/2mmbWvt) cannot be realistically identified in the case of biodiversity with its multiple dimensions (Purvis 2020). As a consequence, the scientific community has to approach the biodiversity crisis from multiple perspectives. providing knowledge, tools and solutions that help optimising the outcome of different goals. This can be achieved by reducing knowledge gaps, synthesizing and conceptualizing the role of biodiversity in providing ecosystem services, and developing a unifying framework to study variation triggered by global change across biological scales. Theory construction should progress in parallel with technological advances for biodiversity monitoring and modelling, and, in close connection with disciplines external to natural sciences, serve to design policies aiming at preserving, managing and restoring habitats and species. This last step is crucial to reduce the mismatch between the scientific evidence of impacts on one side, and policies and societal expectations on the other.

One of the most important knowledge gaps is the quantitative assessment of human effects on ecosystem processes involving interactions among species in the complex natural and social networks where they occur, and their implications for ecosystem functions and the provision of goods and services. These interactions may involve species undergoing geographic range displacement or abundance shifts, and both native and invasive alien species. The status and function of microorganisms and the role of their diversity in ecosystems is another key issue that lack sufficient knowledge. Both species interaction networks and microbial communities represent hidden facets of biodiversity making invaluable contributions to ecosystem functions. On the other hand, the success of conservation planning and ecosystem-based management depends on our ability both to anticipate species' responses to global change and to manage conflicts arising from ecosystem conservation and economic exploitation (farming, fishing, hunting, use of exotic species, etc.). Understanding the social and political contexts underpinning these practices is necessary for sustainable wildlife management and the reformation of

policies integrating environmental issues. Finally, sound empiric evidence builds both on manipulative experiments and on continuous monitoring and evaluation of ecological dynamics. A challenge in this context is the development of next generation technologies for the remote and non- invasive monitoring of species, ecological interactions and ecosystem properties. These include the application of new DNA technologies or remote sensors in satellites, apps, unmanned vehicles, to map variations in the state of biodiversity across time and space.

Here we propose nine challenges for (i) filling knowledge gaps, (ii) advancing technology and (iii) seeking solutions for biodiversity conservation under global change. Palaeontological approaches to the biodiversity crisis are presented in the Strategic Theme #14; we will prioritize here challenging points in which the ecological scale predominates —current and future scenarios— although evolutionary processes are also inherently involved when targeting biological responses to changing environmental conditions. The management of primary productivity is presented in the Strategic Theme #6. We focus here on the conservation of other important services provided by nature, including those provided by wild animals and microbial communities.

2. IMPACT IN BASIC SCIENCE PANORAMA AND POTENTIAL APPLICATIONS

Current explanations and models anticipating responses to global change are often based on knowledge on biodiversity that is incomplete or directly missing for numerous taxa, geographical regions, ecological functions and interactions (Hortal et al. 2015).

Moreover, policies dealing with endangered species and ecosystem conservation often lag decades behind the publication of relevant science. Our key-challenges aim at reducing these gaps through theoretical, technological and policy-relevant advances. The functional properties of ecological systems are multifactorial and interactive. Even if solid theoretical models on how species coexist at the community level exist, they are often disconnected from empirical validations. The composition of ecological communities and the nature of species interactions are influenced by shifts in species geographical distribution and phenology caused by climate, by the spread of invasive species and other global change impacts. Predicting community dynamics under global change involves understanding the effects of different stressors and processes on local species' interactions, while to predict the responses of natural populations we need to know how fast adaptation can occur in novel conditions.

An important obstacle to develop more realistic models of current and future biodiversity distribution is that the data needed to build models are often scarce or absent. Collecting detailed information on millions of species around the world is an infeasible challenge for researchers, and field techniques may fall short of performing large scale and standardized monitoring. Low-cost and non-invasive remote sensors can be developed to monitor biodiversity over time and across different spatial scales as an alternative to human eye and ear. Moreover, high-throughput sequencing methods enable the simultaneous sequencing of thousands of genetic markers across whole genomes and can be used to assess the status of wild populations and species interactions.

Intrinsic positive relationships between biodiversity and the provision and stability of ecosystem services are accepted nowadays, not only among scientists, but also among environmental managers or policy makers. The dual goal of conserving biodiversity and nature's contributions to people is thus in the core of the environmental political agenda (e.g., the EU Biodiversity Strategy for 2030 https://ec.europa.eu/info/sites/info/files/communication-annex-eu-biodiversity-strategy- 2030_en.pdf, the 15th UN's Sustainable Development Goal https://sustainabledevelopment.un.org/). The Convention on Biological Diversity and other biodiversity-related multilateral agreements claim urgent changes in policy and human behaviour to preserve, together with biodiversity, our options for future solutions to global environmental problems (e.g., Aichi targets, www.cbd.int/sp/targets/). The integration of environmental issues into economic and social policies has entered the politic agenda (https://ec.europa.eu/environment/integration/integration.htm). These agreements, actions and policies are important because even when we have the knowledge to perform conservation actions, these need to be coordinated with economical and societal interests to be effective. The call for actions has permeated society deeply, and the COVID-19 pandemic has contributed to a raised awareness about the impact of wild animal consumption and habitat clearing on nature, and the indirect consequences for disease control. Keeping in mind the above demands, the goal of this chapter is to address the current specific challenges necessary to maintain or invert trends of biodiversity loss.

3. KEY CHALLENGING POINTS

3.1. Filling knowledge gaps

Tackling complexity in the relationship between biodiversity and ecosystem services

Global biodiversity loss is a central component of environmental crisis whose consequences largely overcome the simple decrease of species number. Much concern is about the decline of ecosystem functioning and services concomitant to the loss of species and their ecological interactions. Coping with biodiversity decays and properly managing ecosystem services, at the large spatial -but short temporal- scale required by humanity, still requires strong research efforts. Here, we urge, first, to disentangle the structural and functional complexity of the link between biodiversity and ecosystem services and, second, to assess the spatial scales at which complexity operates in real-world landscapes.

Ecosystem services rarely emerge from simple ecological functions provided by single species, but from the joint activity of large assemblages of species structured in complex networks of interactions. Even apparently well-defined services, like crop pollination, depend not only on wild pollinators but also on wild plants providing additional resources to these animals (Figure 1). Therefore, integrating the structure of interaction networks in the biodiversity-ecosystem functioning axioms is essential for re-interpreting the mechanisms that control the provision of multiple ecosystem services (Hines et al. 2015). In fact, different services may be represented as the functional outcomes of different sub-networks or modules, interconnected by common species with multiple roles (García et al. 2018). For example, plants interact with herbivores for biomass production but at the same time drive nutrient cycling with soil microorganisms. Topological measures of interaction complementarity may be thus used for analyzing the effects of biodiversity on simultaneous ecosystem services.

Multiple functions depending on interrelated biodiversity components lead to trade-offs, synergies and feedbacks among ecosystem services. A classical tradeoff is that between agricultural production and agroecosystem services: intensifying agriculture for increasing crop yields leads to decays in natural pollination, pest-control and nutrient-cycling. Trade-offs also may emerge between ecosystem services and disservices, promoted by the same organisms through different functional roles. For example birds exerting pest regulation in crops may otherwise decrease production by damaging fruits. Synergies occur when

FIGURE 1–Ecosystem functions, such as pollination, often emerge from the joint activity of large assemblages of species. Picture by Paola Laiolo.



a given ecosystem service benefits from the increase in other, as for example when enhancing seed dispersal by animals drives vegetation expansion, which results in increased carbon sequestration. Feed-backs are a mechanism of synergism, through circularity in the reciprocal positive effects between interconnected ecosystem services. For example, pollination harnesses from the increased plant growth resulting from nutrient cycling which, in turn, responds positively to the accumulation of organic matter due to plant growth.

Discerning the spatio-temporal scales of the structural and functional relationships between different ecosystem services is also mandatory. Although complexity has been assessed through small-scale experimental and observational research, little is known about its relevance at the large spatial scales at which many services (e.g. water regulation, carbon sequestration) need to be managed. Paradoxically, these large scales are also those at which anthropogenic drivers erode biodiversity. Real-world landscapes must be thus interpreted as spatial mosaics for the interconnected exchange of species, interactions and ecological functions. Managing these mosaics for benefiting simultaneously biodiversity and people requires the integration of interrelated ecosystem services as well as the scaling-up of mechanisms determining the link between biodiversity and ecosystem functioning (Kremen & Merenlender 2018; Manning et al. 2019).

Unravelling the structure and ecosystem functions of microbial communities

In the early 1990s, the International Programme of Biodiversity Science DI-VERSITAS, a programme promoted among others by the International Council of Scientific Unions (ICSU) and UNESCO, and now migrated to both Future Earth (http:// www.futureearth.org/) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), raised public awareness on the lack of knowledge on the diversity of the microbial world. This programme highlighted the crucial role that microbial biodiversity plays in the maintenance of many ecosystem resources and processes that benefit humans, and tried to reach public opinion and policy decisions. DIVERSITAS emphasized the immense genetic diversity of microorganisms and their crucial and unique roles as essential components of food webs and biogeochemical cycles and included "microbial biodiversity" within the nine fundamental cross-cutting research themes of critical importance for biodiversity science. On the whole, the sustained effort carried out for microbial ecologists in the last 30 years circumvented some of the methodological and conceptual concerns that had strongly limited the general perception of how crucial microbes are for Earth biodiversity and functioning, and initiated the effective transplantation of concepts and basic knowledge from the general ecology grounded on plants and animals to microbial ecology. The progress sequentially added on (i) cataloguing microbial biodiversity, and (ii) unveiling of spatio-temporal distributions and patterns. Some emerging facts and trends have already shown the large and multidisciplinary potential of microbial discoveries such as DNA polymerases to successful polymerase chain reaction (PCR), Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR) and advanced genetic engineering, several biotechnological products present in our daily lives, and key microbial species as fundamental pieces to understand the evolution and generation of eukaryotes, among many others. Microscopic organisms have been, however, mostly excluded in conservation studies and microbiology has been developed as a scientific discipline lacking a natural history background. Microbes arise as an important part of the biological richness of any environments that should be considered as a fundamental component of the natural heritage and key components for ecosystems management and human well-being (Figure 2). Interdisciplinary Unified Microbiome Initiatives to understand and harness the capabilities of the set of Earth's microbial ecosystems are expected to raise in the coming years. Interestingly, currently we are only able to identify < 50% of the genetic material recovered from natural microbiomes missing what has been

FIGURE 2–Stratified lakes are appropriate environments for studying the links between composition and functionality in microbial communities. Pictures by Emilio O. Casamayor, Ricardo Guerrero and Xavier Triadó.



informally called the "biological dark matter", formed by genes that have an unknown function. Certainly this "dark matter" is the new and very exciting next frontier to be explored and unveiled, and this challenge needs of powerful computational approaches, large biological datasets and surveys, and improve the basic knowledge in physiology and cell biology. Additional challenges will also need to identify the presence or absence of key microbial species on which the whole microbiome network is articulated and those between which most of the energy and matter of the system circulates, as well as the degree and nature of the biological interactions between the different node components and between micro- and macroorganisms using systems biology approaches. Recent studies show microbial saprophytes and parasites to be more diverse and environmentally recurrent than previously expected, with highly specific interactions and a potential relevant role in food webs that needs still to be unveiled. Understanding the roles of the aboveground and

belowground phytobiome and of the gut microbiome are major challenges to fully understand macroorganims traits such as growth, adaptation to abiotic stresses, immune activation, and behaviour, and on how to modulate these interactions for human benefits.

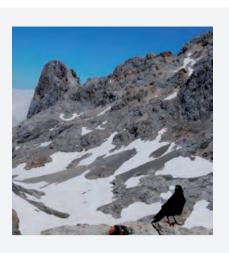
Understanding the ecological and evolutionary dynamics of communities under global change

The dynamics of ecological communities result from the interplay of ecological, evolutionary and biogeographical processes, as local coexistence of individuals and populations is the outcome of their adaptations to the biotic and abiotic environment, and the dispersal from other localities (Soberón 2007). It follows that local communities are, in a significant part, affected by processes occurring outside them. In practical terms, this implies that understanding community dynamics under global change involves understanding the effects of different stressors and processes on local species' interactions, metacommunity dynamics and species distribution ranges. These include:

(i)physiological constrains that determine the environmental conditions at which species can persist; (ii) dispersal and biogeographical processes that determine the localities reached by each species; (iii) resource availability that limits the establishment and growth of local populations; (iv) stochastic fluctuations in species populations due to metapopulation dynamics; and (v) the effect of biotic interactions on species' responses to the environment (Hortal et al. 2010). Under this framework, species traits would (co)evolve along large spatial extents (Thompson 2005), forming a regional pool of species that are then filtered by local conditions determining species coexistence.

The study of species selection is central to understand community assembly and evolution across scales (Vellend 2016). When subject to global change stressors, species will be selected through assembly processes and/or evolve novel adaptations locally to adapt to the new conditions in the community. The greater the stress, the stronger will be the selection of individuals with particular combinations of trait values that allow them to thrive around the new environmental optima (Mason et al. 2013). Two main kinds of selection processes operate under species coexistence (HilleRisLambers et al. 2012). Equalizing processes select individuals and species with similar niches, minimizing their fitness differences along gradients; this happens, for example, when biotic and/or abiotic conditions impose a stress that selects individuals with similar niches (environmental filtering) (Figure 3), or when facilitation

FIGURE 3-Abiotic conditions impose a stress on alpine organisms and select individuals with specific ecological niches (environmental filtering). Picture by Leandro Meléndez.



processes select species with particular traits. Stabilizing processes select for dissimilar niches, maximizing the fitness differences along these gradients; this typically happens in limiting similarity processes, where competition for a finite resource selects coexisting individuals with differing niches and/or phenotypes (Mason et al. 2013). Here, variations in traits of functional importance can help understand the mechanisms behind species selection, and scaling the effect of abiotic gradients and biotic interactions up to the community level (Pausas & Verdú 2010). Stabilizing and equalizing processes would produce different communities, as strong abiotic filters slow down the pace of competition allowing for the co-existence of functionally similar species, while strong biotic competitive interactions select species that avoid trait overlap to escape competition.

However, both types of effects may create similar patterns, as they can select for the same or correlated traits and/or phylogenetically closer species, and superior competitors can also have a disproportionately large effect on other species (HilleRisLambers et al. 2012). There is a significant amount of sound and well-developed ecological and evolutionary theory about all these aspects of selection separately (e.g., Thompson 2005, Vellend 2016). However, their effects are complex and intrinsically scale- dependent, and there is a dearth of information about how they interact and shift in importance as environmental conditions change at different scales. Without such basic information, forecasts of community dynamics under changing conditions will always present a large degree of uncertainty. Part of this uncertainty comes from the lack

FIGURE 4–Integrating observational evidence with experimental evidence of phenotypic trait variation in response to shifts in abiotic and biotic conditions is fundamental to understand species responses to global change. Picture by Paola Laiolo.



of integrative studies that consider several scales and processes simultaneously. Given the complexity of ecological systems researchers have frequently resorted to dividing the system into smaller and more tractable units, thus analysing a set of drivers at a fixed scale. As a consequence, different disciplines have specialised in certain scales developing entire bodies of knowledge based on divergent – and sometimes contradictory– core ideas. Solving this Gordian knot requires combining observational and experimental approaches to help connecting the theoretical bodies of biogeography, macroecology, ecology and evolutionary biology into tractable models that combine metacommunity dynamics of species selection with the evolution of traits and niche under coexistence (Figure 4).

With this challenge, knowledge will advance in three major fronts. First, the integration of different bodies of ecological and evolutionary theory will allow incorporating the complex effects of environment and coexistence into the new evolutionary synthesis. Second, we will get a better understanding of how species and communities adapt to different aspects of global change, with

the associated changes in ecosystem functioning. Finally, enhanced adaptive management of biodiversity through improved metacommunity and species distribution models will increase the reliability of forecasts of biodiversity dynamics under different global change scenarios.

3.2. Advancing technology

Next-generation monitoring: technologies and analytical methods to detect and study the impact of global change on biodiversity

Addressing the formidable impacts of global change on biodiversity requires massively increasing our capacity to monitor different aspects of biodiversity over large spatiotemporal scales. A key challenge is to develop a new generation of affordable monitoring technologies that can boost the amount and quality of data gathered on species, communities, habitats and threats (Pimm et al. 2015). Despite the long tradition of using monitoring technology in ecology and conservation (including some well- established areas like radiotracking, biologging, remote sensing, camera traps), recent advances have brought a staggering range of more experimental applications of technology (from tiny radio-trackers on insects, to continental-scale monitoring of bird migration using weather radar stations) that are not yet widespread.

Research is critical in two linked fronts to address this key challenge of producing next-generation technologies for biodiversity monitoring. First, more work is needed in mainstreaming the use of novel and emerging technologies that are currently experimental or even conceptual. Such technological maturity is achieved by extensive field trials, studies of cost-efficiency compared to traditional monitoring methods, and developing associated analytical and computational methods to deal with the idiosyncrasies of new data types (e.g. false positives) and handle increasingly larger data volumes (e.g. Artificial intelligence-based species identification from pictures and sound files). Technologies with great potential for large-scale monitoring that are undergoing rapid development include next-generation sequencing of genetic material (NGS, see the next challenging point) and acoustic monitoring, particularly surveillance monitoring of environmental change using soundscape-level metrics as early-detection systems. A third opportunity is using technology to unleash the full potential of citizen science (Figure 5).

The second research front is about understanding how to massively scale up the global availability and effective use of monitoring technology. A growing movement is calling for the conservation community to become



FIGURE 5-Acoustic monitoring devices, citizen science programs and unmanned aerial vehicles can help surveying and mapping biodiversity. Pictures by Federica Rossetto and Begoña García.

innovators (Berger-Tal & Lahoz- Monfort 2018) and actively seek to create technologies that are (i) affordable, (ii) field- ready and (iii) offer specific functionalities. Success requires investigating the international leadership, institutions, processes and funding mechanisms that need to be established for the development, production and distribution of targeted monitoring technologies to be scalable and viable over the long term (Lahoz-Monfort et al. 2019). Open-source technology is likely to be instrumental in this process, but to date only a handful of open-source devices for biodiversity monitoring are achieving large-scale uptake (e.g. *AudioMoth* for acoustics, Figure 5). This is uncharted territory and a thorough exploration of some key areas (e.g. business models that support development of affordable "technology for good", public elicitation of technology roadmaps that reflect real monitoring needs, multi-NGO vs. intergovernmental institutional leadership) is essential for collaborative open-source innovation to become a viable reality with global impact.

Next generation monitoring will play a key role in shaping the emerging efforts on modelling in the current biodiversity panorama. Assessing the potential impacts of global changes on biodiversity requires the development of modelling and the use of these models under various scenario assessment frameworks allowing the comparison of likely biodiversity impacts under different future societal trajectories. The current challenge is in developing and evaluating models that correctly capture spatial and temporal dynamics in biodiversity. However, these data are generally scarce to adequately capture these patterns. Integration of large-scale, ambitious, cost-effective monitoring with current modelling efforts developed at different spatial scales emerges as a key target of future integrative efforts in biodiversity research.

Next-generation monitoring of genetic diversity

It has long been recognized by the scientific community that genetic diversity is of fundamental importance for the survival of populations even on a conservation time scale (Allendorf et al. 2010), but genetic diversity has only recently been incorporated into conservation goals and laws, such as the Aichi Biodiversity Targets. In order to monitor genetic diversity in populations of wildlife, it is necessary (i) to broadly sample the populations, and (ii) to measure variability at genetic markers that are sufficiently variable to accurately measure genetic diversity in a way that can be compared against other samplings of the same population (Figure 6).

FIGURE 6-Genetic diversity has been incorporated into conservation goals and laws, thus it becomes important to measure it in ways that are useful for determining if conservation targets are being met. UMIB Molecular Ecology Lab. Picture by Paola Laiolo.



Methods have been developed to sample environmental DNA (eDNA) from soil or water to determine the presence or absence of species (both terrestrial and aquatic; Sales et al. 2020). These studies generally yield a confirmation of presence of a species or genus, based on fragments of single genetic markers, although this is far from sufficient for other scopes, for instance to monitor genetic diversity through time in a population (Forcina & Leonard 2020). NGS technology can help expanding these and other non-invasive sampling methods (e.g., collection of feces, hair or saliva) to anonymously sample the local population of one or more species simultaneously.

Several different genetic markers have been used to measure genetic diversity in populations, and changes in genetic diversity in populations through time. Apart from eukaryote mitochondrial or chloroplast DNA sequences, the most common markers are single nucleotide polymorphisms (SNPs) and microsatellite size polymorphisms. SNPs are distributed throughout the genome, and very many of them can be genotyped, but finding them requires a lot of system specific work which is not easily applicable to other species, or even other populations of the same species. Microsatellites are highly variable, and numerous throughout the genome. Systems set up in one species are often

useful also in other related species. The normal scoring of these loci, however, is very fickle and so results cannot be compared between labs or even projects within a lab.

Introns may be a good in-between marker. There are very many of them distributed throughout the genome, there is a reasonable expectation for variability without prior data, and the primers to amplify them are somewhat conserved and so can be used across many related taxa (Forcina & Leonard 2020). They have not been extensively applied at the population level, likely due to logistics. Until recent advances NGS, it was both very time consuming and expensive to sequence a panel of these markers in many individuals. Now large multiplexes of introns can be amplified in single reactions and sequenced in large pools (i.e. Camacho-Sanchez et al. 2018). The data generated in this kind of project have the important benefit of being easily comparable between projects and labs- a key character of a useful tool for monitoring. Microsatellite loci, discarded above as a good tool for monitoring because of the lack of comparability of genotypes across projects, may also be rescued by NGS. If these highly variable loci could be successfully sequenced instead of the standard size polymorphism, they may be become useful in the context of monitoring. Intron and microsatellite sequencing are less developed, and very much less data is available for comparison, but these are issues that can reasonably be rectified, and monitoring the genetic diversity of populations will in any case require the collection of population specific data on an on-going basis.

NGS methods have strongly advanced our knowledge of microbial communities, although we are still far for a complete catalogue of microbes and its distribution and dynamics on Earth, and this limitation will guide future research in the coming decades. NGS can accelerate the discovery and characterization of microbial diversity, permit establishing reliable databases, collecting and exchanging information on the biological characteristics of microorganisms, and capturing microbial functional diversity. A wide array of powerful techniques has been developed to deal with in situ status of microbial diversity (Casamayor et al. 2002). These include, i) metagenomics - the study of large DNA fragments obtained directly from the environment and the use of highthroughput DNA sequencing and further reconstruction of large pieces of genomes using bioinformatics, ii) comparative genomics - using metagenomes and available genomes in databases to both make inferences about ecology, biology and evolution, and to search for relevant functional genes, iii) functional genes surveys by metatrancriptomics and quantitative PCR, iv) well-analyzed large gene datasets, high statistics performance, and high computational power.

3.3. Protecting biodiversity

Mitigating the impact of invasive species

Biological invasions are considered one of the five most important drivers of biodiversity loss: they affect native species richness and abundance, increase the risk of native species extinction, affect the genetic composition of native populations, change native animal behaviour, alter phylogenetic diversity across communities, modify trophic networks and alter ecosystem productivity, nutrient cycling, hydrology, and disturbance regimes (see refs in Pyšek et al. 2020). Both the numbers and distributions of invasive species are increasing in many parts of the world, to the extent that the biogeographic distinctiveness of different regions is becoming blurred. Furthermore, invasive species are directly or indirectly related to 54% of reported animal extinctions (Clavero & García-Berthou 2005) and are currently listed as a major threat for 27% of Red List species.

To unravel the contribution of invasive species to the biodiversity crisis and mitigate their impacts, we need to advance in three major fronts. First, we need to improve basic knowledge. Past research on biological invasions has mainly focused on the ecological factors determining success and distribution, focusing on particular species, habitats or ecosystem functions, and on short-term consequences. In contrast, the interaction of invasive species in complex networks, and their impacts on ecosystem services and human health have received little attention. Moreover, current knowledge is strongly biased towards terrestrial habitats and services that have marketable values (agriculture yields, forestry production, human health), whereas aquatic habitats and nonmarketable services are largely ignored (Gallardo et al. 2019). Furthermore, long- term consequences of past and current invasions remain largely unknown. These gaps in knowledge remain pervasive challenges that hinder the effective prevention and management of invasive species. In the future, it will become increasingly important to integrate evidence across habitats (terrestrial, freshwater, marine), scales (local to continental) and impact outcomes (on biodiversity, ecosystem services and human well-being).

Second, we need developing future scenarios of invasion. In contrast to other drivers of global biodiversity loss, such as climate or land use change, we still lack a thorough understanding of the potential numbers and impacts of

invasive species on biodiversity and human livelihoods for the decades to come. Future scenarios would set up a baseline against which to compare the effectiveness of management interventions, to anticipate the number of invaders and their associated impacts under a range of future climate or socio-economic scenarios, and to compare the ecological and economic costs of "best" against "worst" case scenarios. This challenge will require additional data to update and complement global databases of biological invasions, particularly for underrepresented taxonomic groups, such as microorganisms. It will also require an understanding of the synergies between biological invasions and other drivers of change such as transport, climate, land-use and socio-economic developments, and their context-dependencies. Such scenarios are fundamental not only to direct future research but also to support policy and management.

Finally, we need screening methods. Part of these methods are described above, here we outline those specifics for invasive species. The arrival of these species is extremely difficult to detect, and once established, they are very challenging, often impossible, to eradicate. New technologies are emerging that can support early detection, including environmental DNA, drones, robots, light-based technologies, acoustic detection, e-nose devices, nanobiosensors, artificial intelligence, smartphones that facilitate citizen science, syndromic surveillance of social media, big data analysis to detect patterns, remote sensing and satellite imagery (see Martínez et al. 2020 for a review). Novel technologies also offer invaluable opportunities to mitigate the impacts of invasive species, through for instance, biological control, robot manipulation, synthetic gene drives, virtual fencing, anti-fouling coatings, new and more sustainable toxicants that would allow an early response to upcoming threats. The challenge is not only to develop these technologies, some of which are already being used successfully (e.g. Wangensteen et al. 2018), but rather to scale up their widespread deployment and implementation, ideally integrated into a national biosecurity monitoring network.

The three research fronts outlined above are highly inter-related and constitute a bottom up approach from the laboratory or field site to the market, directed to improve the prevention and management of biological invasions, thereby protecting biodiversity and ecosystem services.

Halting the loss of pollinators

The so often called "pollinator crisis" provides a textbook example of a conservation issue with far reaching implications for ecosystems, the economy and our society. As such, it is illustrative of how different sectors can work together to solve a common problem. Pollinators were a largely ignored component of biodiversity until early 2000's, with most conservation actions devoted to large mammals, birds and other iconic species. A parallel recognition of their role in ecosystem functioning (i.e. mediating the reproduction of > 80% of plants) and ecosystem service provision (i.e. maximizing production of 75% of crops) along with initial observations of pollinator population declines triggered a scientific and societal alarm. As a result, the conservation of pollinators has acted as an umbrella to conserve other neglected but important invertebrates and has achieved key conservation milestones, including changes in policy regulations in agricultural habitats. However, despite recent advances, we are still far from understanding or reverting pollinator population declines.

Pollinators are a diverse group of animals, potentially responsible for reproduction of more than 80% of plant species worldwide (Ollerton et al. 2011). Bees are generally considered the most important pollinators, especially for crops (Klein et al. 2007).

However, many other animals provide pollination services, including other groups of insects like Coleoptera, Lepidoptera, Diptera and non-bee Hymenoptera. In addition, birds, bats, rodents and even lizards are pollinators of many plants, especially at lower latitudes (Winfree et al. 2011). However, despite increasing concern about the decline of pollinators worldwide, data on population trends are scarce and often geographically and taxonomically biased (Bartomeus et al. 2018). For example, a recent IUCN report concluded that even for Europe's comparatively well-studied bee fauna, more than 55% of bee species fell into the 'data deficient' category. Hence, we first need to monitor populations to assess the current status of species. As in many other taxa, researchers have now developed strong consensus that disturbances such as habitat destruction, land-use intensification, chemical exposure, exotic species and climate change are causing pollinator declines and often act synergistically (Goulson et al. 2015). We need to integrate this knowledge into conservation actions that actually work for pollinators. This is more easily said than done, as theoretical models are often disconnected from empirical studies, and our predictive ability on how entire communities will respond to conservation actions is poor.

Finally, pollinator conservationists have advanced a lot in societal awareness, facilitating the development of pollinator friendly policies. However, current

research shows that without integrating economic sectors (e.g. farmers), the wider society (e.g. NGOs), policy makers and conservationists into the conversation, efforts to change how we manage the landscape for pollinators are unsuccessful and that despite regulations, our farming systems are still unfriendly to wildlife. We still need to walk a long road to create multi- and trans-disciplinary teams that transform conservation actions into win- win situations. Ecological researchers cannot do this alone and need to team up with social scientists and involve all relevant stakeholders. Reversing the pollinator crisis will not only be a great conservation success, with direct implications for human well- being, but will teach us a lot about how to leverage ecological information, public engagement and economical decisions to achieve meaningful conservation actions in other taxa.

Linking ecological and social research for managing wild vertebrates for healthy ecosystems

Wild vertebrates are an integral part of biodiversity, and are involved in many of the services provided by the ecosystem not described in other points. For example, they play key roles in nutrient cycling (i.e. supporting services), actively participate in disease regulation (i.e. regulating services), provide food and materials used by people (i.e. provisioning services) and are important for recreation, tourism, and cultural uses and for aesthetic reasons (i.e. cultural services) (e.g. Whelan et al. 2008) (Figure 7). The conservation of wild vertebrates is threatened by many components of global change due to habitat loss, over-exploitation by humans, invasive species, pollution and climate change (IPBES 2019). Wildlife loss has consequences for ecological processes that support biodiversity and may have also serious socioeconomic impacts. The maintenance of wild populations of vertebrates in humanized landscapes such as Western Europe sometimes needs active management of their populations or their habitats (this is clearly the case when considering endangered species). However, management aimed at increasing their numbers can come into conflict with other human activities like farming or hunting (Redpath et al. 2013). On the other hand, populations of some wild vertebrates have increased substantially in recent decades (as a consequence of human-induced changes in the environment, or directly from management actions), and impact human livelihoods or even other species or natural processes in the ecosystem (e.g., invasive alien species of birds and mammals, increasing populations of certain ungulates, particularly wild boar, etc.). In these cases, management to maintain populations under certain levels is sometimes seen as one of the options to reduce these impacts (Martínez-Jauregui et al. 2020).



FIGURE 7–Wild vertebrates are an integral part of biodiversity involved in many ecosystem services. Picture by Alberto Fernández Gil.

However, the increase in society of certain values such as animal welfare or even attributing to wildlife the same rights as humans implies that parts of the society may strongly oppose this management, despite the ecological damage arising from not doing it (Martínez- Jauregui et al. 2020), which may render ecologically-efficient solutions a source of social conflicts. Conflicts over wildlife management are increasing and are often costly to both humans and involved wildlife species (Redpath et al. 2013), and therefore their effective mitigation through scientific solutions should be a priority.

Sustainable wildlife management, understood as the management of wildlife species to sustain their populations and habitat over time with consideration to the socioeconomic context in which it is implemented (Cardador et al. 2015), requires a good understanding of both the biological/ecological as well as the socioeconomic systems, and this can be only achieved through a multi-disciplinary approach that integrates the natural and social sciences (White et al. 2009). A key scientific challenge is to find situations that are both ecologically efficient and socially acceptable.

Increasing our understanding on human-wildlife relationships and how these have evolved is critical, particularly in this period of global change in which

most people live in urban areas. A major challenge is assessing the positions and preferences of the society towards different alternatives of wildlife management in terms of efficiency, cost and human-ness, particularly in the face of uncertainty in relation to the ecological efficiency of different alternatives. Reducing that uncertainty (through better understanding of the relationships between species in the community and their environment, and response to human-induced changes in that environment) is another crucial challenge.

Nature conservation through laws and policies

Conservation laws and policies, adopted by human institutions at (sub)national or international levels, are aimed at forbidding or regulating human activities that negatively impact ecosystems, habitats and species, in order to slow or stop the degradation of nature. Some of them aim for the recovery of nature such as, for example, the US Endangered Species Act, the EU Habitats Directive, or the Convention on Biological Diversity. Conservation laws and policies are increasingly recognized as important elements of the available toolkit for an effective preservation of nature.

However, the political decision of adopting a given conservation legislation alone is not a guarantee of success in conservation, and the current practices in the implementation of these instruments do not appear to be able to avert the current biodiversity crisis significantly. For example, the recently released 2020 evaluation of the IUCN Red List shows that 22% of the mammal species evaluated (5,899) are threatened. The world's nations previously failed to meet targets agreed in 2002 to achieve a significant reduction in the rate of biodiversity loss by 2010, and are unlikely to meet in 2020 the Aichi targets agreed under the Convention on Biological Diversity. It is also uncertain how current debates on possible targets for the future will avoid the same observed failures.

This situation raises the question of whether, apart from some particular cases, existing conservation instruments are fit for the purpose of preserving populations, ecosystems, and nature, and if and how their effectiveness could be improved. Although theoretically conservation laws and policies seem effective tools for conservation, and integrating environmental concerns into sectorial policies is a priority for sustainable development for many nations, several pitfalls still jeopardize the power of these instruments, such as poor coordination at national and subnational levels, failures in the integration of the best available knowledge, interpretive uncertainty, implementation,

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compliance, transposition or enforcement failures, or the weakening of these instruments (López-Bao & Margalida 2018). Imperfect legislation can result in distrust and decreasing compliance, and even leading to conservation conflicts. The increasing interest among conservation professionals in boosting the effectiveness of conservation laws and policies requires addressing these limitations, strengthening the interface between conservation science and policy-making. If human societies aim to find a balance with nature preservation, we need to understand, implement and enforce conservation laws and policies properly. Why does conservation succeed in some countries but fail in others? Answering this question will require effective inter- disciplinary approaches, promoting the intersection among ecology, law, policy, and social sciences (which aim to understand compliance and societal norms beyond policy). There is a challenge in understanding the range of measures used by different nations to ensure the effective implementation of conservation laws and policies. This endeavour would benefit from global assessments of the state of the effective implementation of these instruments.

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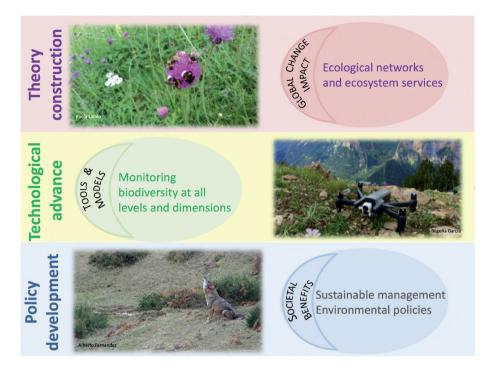
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