

N

New Paradigms for Modern Biogeography Conservation



Diogo Alagador

Rui Nabeiro Biodiversity Chair, MED:
Mediterranean Institute for Agriculture,
Environment and Development, Universidade de
Évora, Évora, Portugal

Definitions

Biodiversity conservation is a relatively recent, synthetic field that applies the principles of ecology, biogeography, population genetics, economics, sociology, anthropology, philosophy, and other theoretical disciplines to the maintenance of biodiversity worldwide.

Conservation biogeography concerns the application of biogeographical principles, theories, and analyses, being those concerned with the distributional dynamics of taxonomic units individually and collectively up with their relevant limiting processes, to problems concerning biodiversity conservation.

Systematic conservation planning is a comprehensive and scientifically sound method aimed at providing decision support for choices between alternate conservation actions. Spatially, it entails a set of stages for choosing, locating, configuring, and implementing conservation actions (protected areas in particular), such that the benefits of the actions therein exceed specified amounts of ideal

protection of biodiversity features and processes. Optimization procedures are key in providing planners the very best efficient and effectiveness solutions.

Aichi Target 11 refers to a global protected area coverage target, established under the Convention on Biological Diversity in 2010. It states that, by 2020, at least 17% of terrestrial areas and 10% of coastal and marine areas need to be protected through effective, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures. For 2030 a new target is being developed with preliminary advices supporting a 30% protected area coverage for both terrestrial and coastal/marine realms.

Global change entangles the worldwide impact of human activity on the key processes that govern the functioning of the biosphere. These include the climate system, stability of the ozone layer, cycles of elements and materials (such as nitrogen, carbon, phosphorus, or water), the balance and distribution of species, and ecosystems and their underlying processes.

Introduction

The planet is changing, and the fast dynamics is jeopardizing human existence. The combined and accumulated effects of ecosystem exhaustion and rapid climate change (CC) are shifting the planet toward new, unpredictable equilibria, possibly

outside the boundaries of human adaptability. Recently, governments worldwide appealed to the urgency of aligning human development with healthy ecosystems. Biogeography, a discipline that systematizes knowledge about the past, present, and future distributions of biodiversity, their triggers and threats, emerges as fundamental to guide the design of effective conservation strategies. The present chapter presents a synthesis about the use of biogeography for the protection of life on land. It starts by summarizing man-made impacts over biodiversity since the deep past; it continues emphasizing the importance of protected areas (PAs) for biodiversity protection and persistence and approaches for their establishment. Particular attention is given to optimization models as they provide guidelines for minimization of (financial) resource spending and/or maximization of ecological benefits. This chapter ends with a close look to the scientific basis of conservation planning, where biogeography explores opportunities for innovation, growth, and expansion. Particular focus is given to the evolutionary pathway of conservation plans, from static to dynamic, from responsive and descriptive to precautionary and predictive, from unidimensional – centered almost exclusively on biodiversity conservation – to the more integrative plans, where other environmental, socioeconomic, and political concerns are unified. This synthesis navigates through the wide spectrum of problem complexity, data requirements and model strategies that are being implemented at different geographic and temporal scales (Fig. 1). Unifying biogeography conservation with other disciplines paves the way to positive scenarios of action, increased awareness and practical and effective responses to bolster long-term persistence of biodiversity on land.

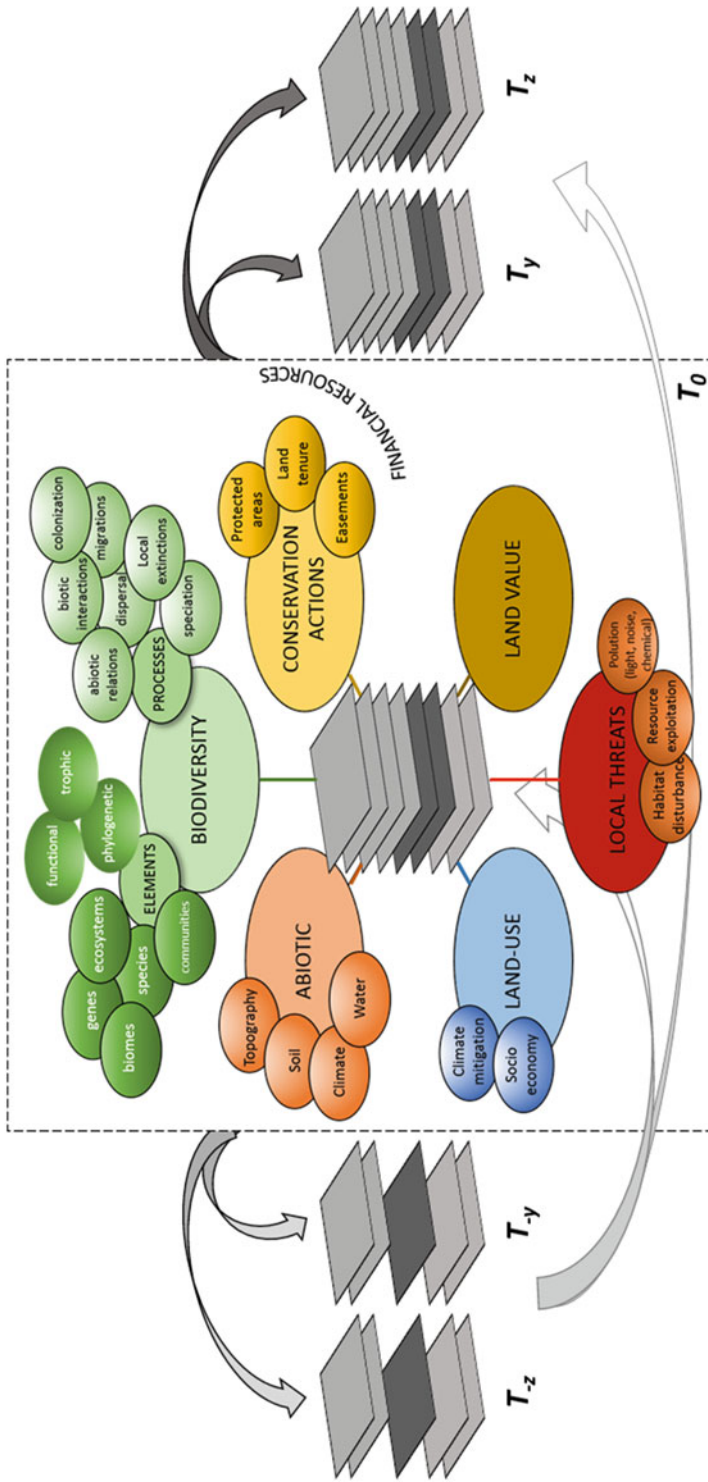
The Planetary Crisis

During the last phase of the Ice Age (50,000 and 10,000 yr. bp), almost 200 large-bodied mammal species went extinct. That was half of the world's mammals weighing more than 44 kg perishing in a short time period. By that time, the planet was crossing a period of CC that was already

compromising some species. A possible combination of human exploitation of populations already compromised by climate-driven environmental changes (or vice versa) may have prompted the great quaternary extinction event (Lorenzen et al. 2011). Some scientists have also suggested that the Ice Age megafauna extinctions set the stage for the planet's sixth major extinction event, which is unfolding before our eyes.

Only in the nineteenth century, Wallace acknowledged what has become one of the key points of conservation biology: biodiversity was not made for humans, nor by them. Biodiversity was considered to incorporate an intrinsic existential value. This new vision settled the ground for the development of the modern conservationism that has started with the industrial revolution and Napoleonic wars, when concerns about forestry exploitation and crop management become generalized. By that time, there was also a rise of conservation concerns in other regions out of Europe. The world's first protected area (PA) opened in 1778, in Mongolia (Bogd Khan Uul, today a UNESCO protected biosphere) and, nearly a century after (1872), the second PA was established in the Yellowstone National Park.

In the middle of the twentieth century, a series of subdisciplines in biology, such as evolutionary biology, genetics, taxonomy, ecology, demography, and biogeography, associated with mathematical modelling to found the "Theory of Island Biogeography" – a branch of conservation biology. MacArthur and Wilson (2001) showed that the number of species in an island varies according to its area and the distance from large land masses. Expanding the island concept to isolated habitat patches on land surrounded by highly disturbed landscapes, the "island paradigm" allowed the effects of habitat loss and fragmentation over terrestrial biodiversity to be evaluated (Richardson and Whittaker 2010). The real extent of the ecological crisis and the need to rapidly increase habitat condition for the sustainment of biodiversity at long-term were finally uncovered.



New Paradigms for Modern Biogeography Conservation, Fig. 1 A schematic summary about a large set of factors that are addressed in biogeography conservation. The arrows establish the flow of information that may exist if predictive models are applied to assess factors in past (T_z , T_y), present (T_0), and/or future (T_z , T_y) times. For many factors deep past information may not exist (e.g., land value), and therefore less data layers are available. For illustrative purposes the darker layers refer to biodiversity informers (either elements or processes)

The Rise of Biodiversity Conservation

Protected areas are the most successful and pervasive conservation strategy implemented. In the last 60 yrs., global coverage of PAs increased from 2,000,000 km-sq to the current 20,400,000 km-sq, equivalent to 15.1% of Earth's land surface (WDPA 2020). Yet, this astonishing expansion still does not fulfil the commitments made by countries under the 2010 Convention on Biological Diversity (CBD 2011). From one side, PA coverage falls short to the agreed 17% of terrestrial land to be protected by 2020 (the 11th Aichi Target). From the other side, many of the established PAs are largely ineffective, which also goes against the commitment letter of "(establishing) *effectively and equitably managed, ecologically representative and well-connected systems of PAs.*" Most of PAs are "paper parks," used by governments as self-proclaimed instruments with reduced conservation success. Typically, PAs are in remote regions with low socioeconomic profit, low agricultural aptitude, and harsh weather conditions. Most PAs coincide with low disturbed regions (Joppa and Pfaff 2009), thus leaving most of threatened species and habitats out of protection.

The recognition of the need to strength PA performance and the realization that the design of effective PAs is far from intuitive prompted conservation planners to move beyond ad-hoc decisions to work under a coherent and comprehensive framework, to assist decisions about how, when, and where to invest in conservation, such that the greatest benefits are met. These principles set up the basis of systematic conservation planning – a discipline that aims to establish effective networks of PAs capable to set biodiversity aside from its most impinging threats and to deliver informed and alternative options that allow managers and planners to tackle the complexity of the environmental system (see below). Margules and Pressey (2000) called for the need to take a rigorous action to protect biodiversity, based on transparent and quantitative approaches, with scientific guidance rather than on political intuition.

Responding to the urgency of rising efforts and investments, several conservation agents have

carried out priority setting exercises to decide where or how to conserve (Redford et al. 2013). Several NGOs have also used scientific guidelines to develop the concept of megadiversity – a group of organisms requiring global conservation focus. Each NGO explored and divulgated their proper concerns using maps that cross different visions on biodiversity in terms of their irreplaceability (the quality of features being unusual, unique, and hardly replaceable) and vulnerability (the degree to which a feature, process or system is susceptible to, and unable to cope with, injury, damage, or harm) (Brooks et al. 2006).

The establishment of global conservation priorities was influential in directing resources toward broad regions. However, they had little success in informing actual implementation of PAs. Separate processes are necessary to identify actual conservation targets and priorities at much finer scales. At these scales, the most impingent threats are distinct, and several local constraints, neglected at global scale, are present (legal apparatus, land markets, conservation players, development priorities, etc.). Bottom-up information flows for identification of priorities are therefore essential to ensure the implementation of area-based conservation. Top-down assessments are important to identify large-scale opportunities of collaboration and to full explore the possibilities of shared efforts to increase the effective protection of biodiversity.

Broadly, the scientifically driven identification of PAs relies on two optimization paradigms. The "minimum set cover" highlights the set of PAs of minimum cost, where all features are adequately covered. Under the "maximal coverage," final solutions warrant that the maximum number of biodiversity features is covered by PA when a fixed conservation budget is available. Using these models as central descriptors of final solutions, other studies added other requisites to best fit solutions to the rules of good PA design from the "Theory of Island Biogeography": PA configuration, extent, and fragmentation (Williams et al. 2005a).

Ecological Processes

Although the consideration of biodiversity patterns concentrates most of the research efforts, the integration of biodiversity processes has also been matter of discussion. Biodiversity processes encompass the ecological and evolutionary processes that maintain, sustain, and generate biodiversity within a region.

Metapopulation Dynamics

At some point of its range, every species suffers, at various levels, the impacts of habitat fragmentation as a result of two factors: low tolerance to local disturbance and excessive levels of disturbance. In these regions, suitable habitats are distributed as isolated patches that experiment intense demographic turnover, resulting from the net effect of colonization, extinction, and dispersal events (Hanski and Ovaskainen 2000). This (meta-) population structure is frequently present at species' range edges, where populations evolve close to their tolerance boundaries, thus leading to small population sizes, high fragmentation, low intraspecific competition, and movement limitations. Interactions among these processes play nontrivial roles in determining not just the presence but also the persistence of a species (Ovaskainen and Hanski 2003). These issues gain particular emphasis under CC (see below), because the success of species to find and explore their tolerable climates is dependent on metapopulation responses at the rear and leading edges, relative to climatic gradients (Anderson et al. 2009).

The characterization of metapopulation dynamics of a single species is a hard task, because demographic responses vary spatially, depending on the genetic, phenotypic, and habitat characteristics. The integration of metapopulation dynamics in conservation plans is not easy, but efforts have been made to analyze a few species in very localized regions, to infer about the patches to prioritize, such that the local species persistence is maximized, the occupancy is maximized, or the number of patches that fell down an occupancy threshold that limits species persistence is minimized (Bode et al. 2008).

Migratory Movements

Some species present seasonal migratory movements. For these, conservation plans need to rely on the connectivity of suitable habitats and on the timings of movement. The use of track record devices in a small number of individuals informs about the trajectories of full populations. When these data exist, the quasi-continuous migratory trajectories are well described using network theory (Xu et al. 2019). In such a network, traversing and stop-by locations, their pairwise distances, and environmental suitability are represented by vertices, arcs, and weights on graphs, respectively. Finding the trajectories that cross the most suitable areas in the right timing and that are used by the largest number of individuals (and/or species) replicates well-studied maximum flow problems in networks (e.g., Iwamura et al. 2013).

For most of species, data for a full migratory trajectory do not exist. In these cases, instead on quasi-continuous movement lines, trajectories are evaluated using the aptitude of discrete regions to support movements along migratory pathways. In these cases, the identification of suitable migratory pathways has been conducted using the standard "minimum set cover" or the "maximal coverage" area selection frameworks (see above), supplemented with connectivity requirements. For example, Johnston et al. (2020) used distribution maps of 41 species of migratory shorebirds breeding in North America, and, instead of representing each species as a single feature, they partitioned species distribution by their timings of occupancy and used each of these partitions as features to be represented (by a given amount) in the final solutions.

Trophic Relationships

The distribution of a species can potentially affect the distribution of other species due to their trophic interactions (e.g., predator-prey relationships). The integration of trophic relationships in conservation area prioritization provides planners ecologically relevant information for the persistence of species and robust trophic structures. Fordham et al. (2013) used dynamic population models to analyze the relationship between rabbits, the Iberian lynx, and diseases of both species.

Using distinct setups on where to prioritize conservation investments and on the areas where seed populations of lynx should be installed, they inferred about population response of the species in the future, using CC scenarios. Decker et al. (2017) modelled freshwater fish assemblages in the Danube River Basin. They divided species into two groups – predators and preys – and assigned larger selection cost to the planning units carrying higher proportion of predator populations. After defining representation targets for each prey species, they solved the “minimum set cover” model to identify the areas with the least predation stress, where each prey species is adequately represented.

Genetic Variability

Species are generally considered homogeneous biodiversity units. However, most species present some level of spatial structure in what respects to phenotypic, ecological, and genetic divergence. Historically isolated populations may represent intraspecific units carrying unique genetic diversity, worth of protection. Diniz-Filho et al. (2012) used alleles present in specific genes of a tree species endemic to Brazilian Cerrado as conservation units for protection and found the smallest number of local populations that carry all alleles, in at least one location (the minimum cost cover model), while maximizing the amount of natural habitat around those population spots.

Two types of genetic load need to be distinguished at the intraspecific level. The vicariate (null) genetic component stores the historical population structure and, therefore, characterizes the ability of populations to respond to future selection pressures (i.e., long-term conservation needs). The adaptive genetic component of populations addresses the microevolutionary events occurring in the recent history (Carroll and Fox 2008). Spatial information for both types of genetic variability (i.e., phylogeography) is critical for effective conservation planning. Vicariant genes are used to define lineages (i.e., genetic trajectories as selection units) to inform which deep evolutionary pools are adequately protected. The adaptive genes that inform about individual fitness and population viability in

current and future environments relate mostly to population persistence. Several studies have shown that intraspecific genetic diversity is spatially structured and that areas of high genetic diversity are often coincident among several species, resulting in hotspots of genetic diversity (Moritz and Faith 1998).

Phylogenetic Pool

When considering multiple species, apart from the intraspecific responses that safeguard population level robustness, (phylo)genetic relationships between species also carry fundamental information (e.g., Carvalho et al. 2017; Thomassen et al. 2011). Widening the phylogenetic spectrum represented in the areas to protect is a good indicator of community resilience (Chao et al. 2014). If one assumes similar evolutionary potential for closely related species and larger differences among distantly related species, higher phylogenetic diversity within a community increases the chances of having some species or clades with high evolutionary potential in the community. This “insurance effect” is not a simple effect of species richness (i.e., having more similar species increases the chances of having successful species in unpredictable environments) but rather an effect of phylogenetic diversity itself (Carroll and Fox 2008).

Functional Patterns

Conserving a diverse set of relevant traits related with important ecological properties of a particular community or ecosystem (functional diversity) enhances adaptability and maintenance potential. Two mechanisms underlying such effects have been suggested (Lefcheck et al. 2015). Trait complementarity instigates niche partitioning and ecological facilitation and leads to a more efficient use of resources within ecosystems. Trait selection describes how more diverse ecosystems have a higher probability of including functionally efficient species. Ecosystem functions represent processes that regulate the flux of energy and matter through the environment (e.g., primary productivity, nutrient cycling, and decomposition). They provide important clues about the benefits provided by the ecosystems to humans (e.g., water

and air quality, provision of food and wood). Chan et al. (2006) undertook a study in which the maximization of returns from ecosystem services guided the selection of areas to prioritize in the Central Coast ecoregion in California. Additionally, the areas to select needed also to guarantee the coverage of some environmental features (i.e., seven ecological classes summarizing information about vegetation distribution, climate, and physiography) and of six ecosystem services (carbon storage, crop pollination, flood control, production of forage for grazing rangeland livestock, outdoor recreation, and supply of fresh water).

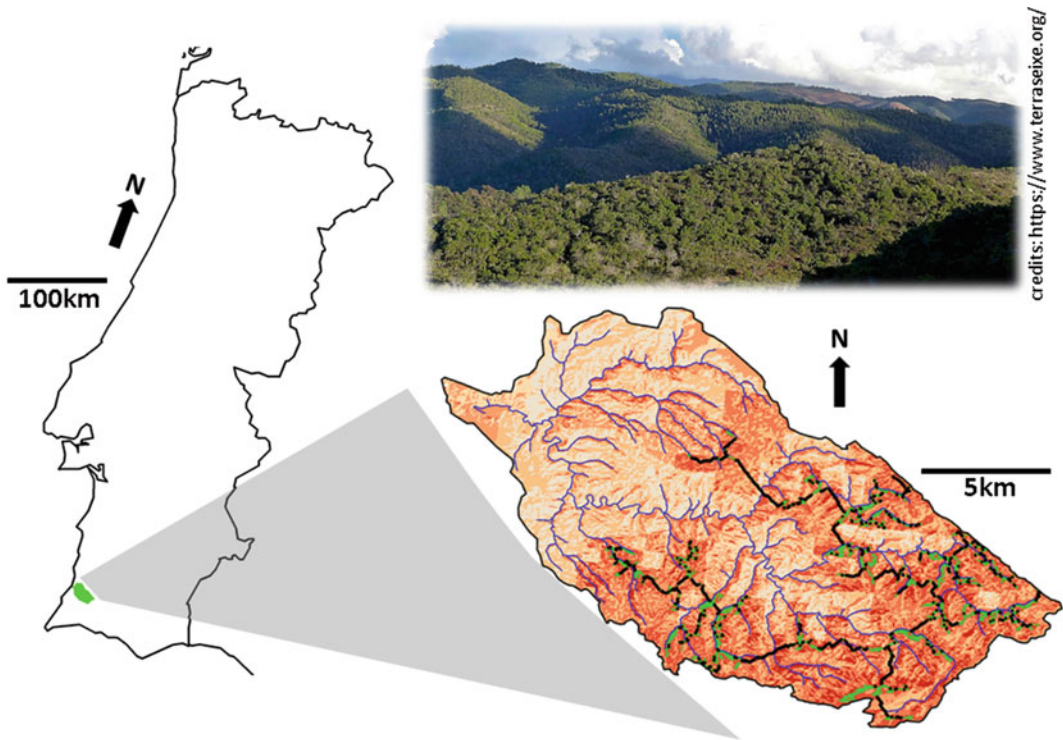
Abiotic Environment

When data representing biodiversity patterns and processes lack, or are not consistent among features, abiotic settings have been used as proxies. Justifications for the use of abiotic settings as conservation targets include (1) their possible broad correspondence with the distribution of biota; (2) their value in informing about areas that potentially support the persistence of species in the face of climate change; (3) their stability over time, as contrasted with current communities; (4) the availability of consistent spatially explicit datasets; and (5) (for some abiotic factors) their large overlap with evolutionary processes, with paramount importance for increased genetic variation (e.g., speciation centers). Speciation centers occur mostly in transition zones, like edaphic interfaces where specific juxtapositions of soil types occur. Interfaces between acid and alkaline soils promote the separation of populations with distinct selective regimes (e.g., fire, water content) and provide conditions for new lineages of plants and animals to evolve and distinct functional communities to appear (Cowling and Pressey 2001). Upland–lowland interfaces associate with ecological diversification of plant lineages and, consequently, of animal lineages. These interfaces are also important in facilitating seasonal movements of fauna between uplands and lowlands and for local-scale adjustment of species distributions to CC (Midgley et al. 2003). The size of the planning region has, most often, driven the type of abiotic surrogate used. In large planning regions, variables reflecting

climate and surface geology have commonly been used. In smaller regions, variables such as slope, exposure, elevation, wetness, grain size, soil geomorphology and chemistry, and local landforms have been preferred – geodiversity. Beier et al. (2015) reviewed 14 studies that used abiotic surrogates for plan development and found that selection sets based on abiotic surrogates performed better than random at capturing known biodiversity in 43% of the cases reviewed. Drought and climate refugia that, by their location and abiotic settings, have been quite stable in the past are also likely to be important stability points in the future. The stability of abiotic variables confers them robustness (i.e., low uncertainty), an important property to be used in anticipative conservation plans adapted for CC (Fig. 2). Studies using abiotic factors as features to preserve identify networks of representative geophysical stages upon which communities transform and develop. To sustain biodiversity, these networks need to capture the spaces where species will evolve and to provide spatial coherence and connectivity to maintain natural ecological flows.

Forward-Looking Conservation Planning

Some of the previous factors empower PAs to buffer the negative impacts from CC. However, they do not integrate plausible species-specific responses in future times (e.g., how species ranges are expected to change). Spatially, a species may exhibit three types of adaptive responses to CC: (1) stability, in areas where the magnitude of local change is still tolerable; (2) displacement from current occurring areas to suitable, neighbor ones (if species dispersal rates, habitat connectivity, and CC velocity permit); and (3) extinction in the areas where none of the two previous responses exist. Because each species possesses its own adaptability potential, either through local tolerance or dispersal mechanisms, major CC typically results in resorted species pools and new species associations, which instigate novel species interactions. Net results of CC effects over ecosystems were recognized in the 1980s (Peters



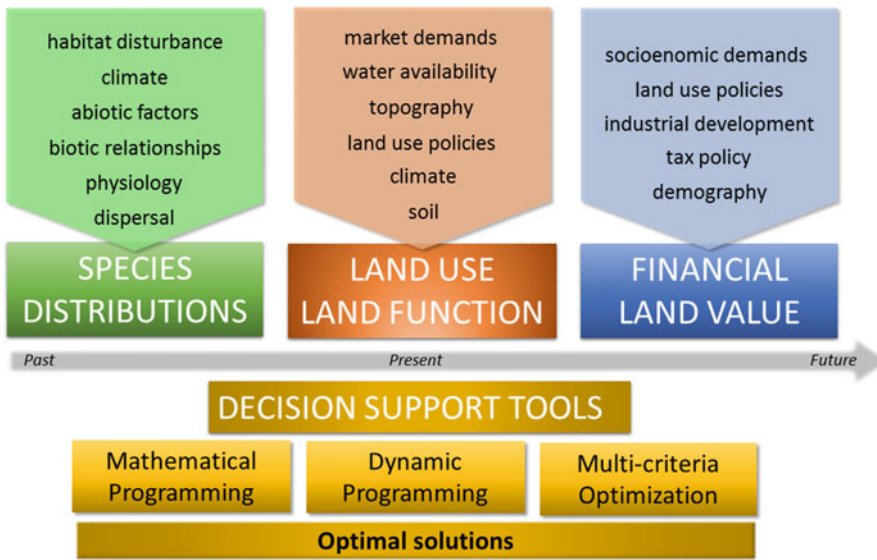
New Paradigms for Modern Biogeography Conservation, Fig. 2 Climate-robust connectivity paths (black lines) linking predicted future climatic refugia (light green patches) in the Seixe river basin in southwest Portugal (see www.terra-seixe.org), Seixe river in blue. The robustness index to climate change (the yellow to red color gradient,

expressing increasing robustness) was obtained using a composite index of predicted stability of the lowest temperature zones up to 2050, topographic roughness, sun exposition (preference to west and northward slopes), and occurrence of Natura 2000 sites

and Darling 1985), but only 20 yrs. later, Hannah et al. (2002) came up with the first analyses on the effects of CC over PAs. With rearrangements of species' ranges, life cycles, population dynamics, ecological interactions, and open doors for invasive species, the ability of PA networks to conserve the species and habitats for which they were created becomes compromised.

The availability of several spatial datasets predicting the distribution of climatic variables in the future and the wide dissemination of models that relate climate with species occurrences (i.e., bioclimatic niche models, Guisan and Thuiller 2005) (Fig. 3) paved the way for researchers to appraise the effects of species-specific responses to CC on PAs and to verify which species are likely to experiment increasing or decreasing PA coverage in the future (Araújo et al. 2011). Climate change

enlarges the functional area of species at long term, implying the expansion of current PAs to new zones and the promotion of cohesive and coherent PA networks. These expansions expand the risk of conservation goals to conflict with established socioeconomic activities. Because of this, trading off PA coverage, protection hardness (i.e., a gradient of accepted activities), and conservation targets define the cocktail that characterizes modern conservation plans (Alagador and Cerdeira 2018; Jones et al. 2016). The identification of the areas that are likely to be suitable for several species in current and future time periods has been executed in two ways. The majority of studies identify those area patches where the largest number of species is able to spatially adapt in the time horizon of analysis. A few studies go deeper in the analysis to explicitly pinpoint the



New Paradigms for Modern Biogeography Conservation, Fig. 3 The main analytic tools used in modern biogeography conservation assessments. The upper arrows accommodate the main drivers of species distributions, land use/land function, and financial land value across time (from past to present and future). After the

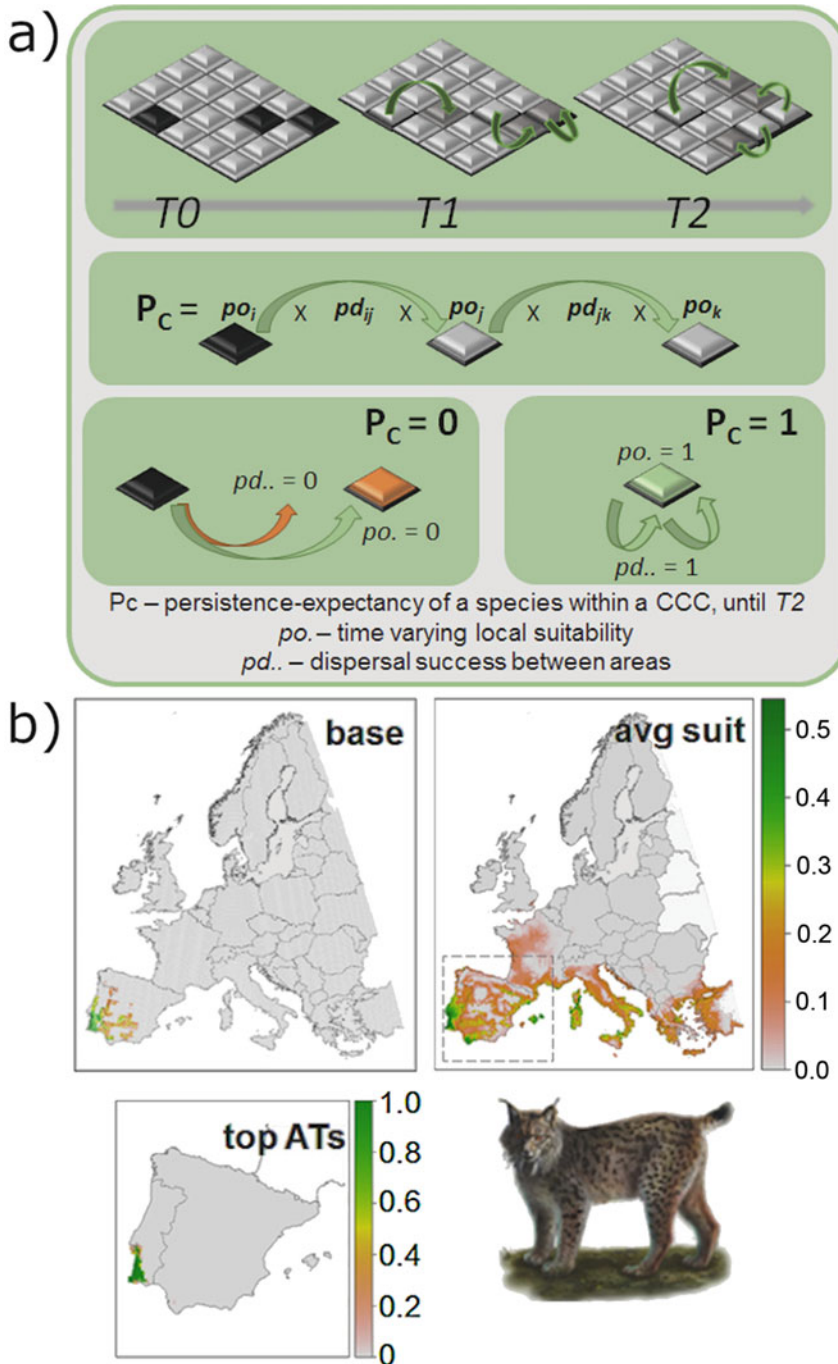
characterization of the socioecological system, decision support tools are implemented to find optimal solutions for the where, when, what, and how questions. The method to use (mathematical programming, dynamic programming or multi-criteria optimization) depends on the nature of the conservation plan

areas that define adaptive movement trajectories of each species (Williams et al. 2005b). Here, the conservation value of each area in a period of time within the trajectory is evaluated and complemented with dispersal functions to retrieve a persistence expectancy of each species in each single trajectory (Alagador et al. 2016). These trajectory models embody two controversial mechanisms. First, the evaluation of areas in a timeline may imply that areas, that were initially considered important and were part of a solution in a given period of time, may exit conservation focus, and the associated conservation cost saved or transferred to a new set of areas with higher conservation benefit, to be protected at future time (i.e., dynamic PAs, Fuller et al. 2010; Alagador et al. 2014). Second, climate-adaptive trajectories may be used to inform where and when assisted colonization of some species should be undertaken in order to maximize the total persistence of the species in the conservation plan (Fig. 4).

The majority of spatial conservation studies for CC have been conducted using a simplified, binary view of conservation options, looking for

the areas to protect (or not). They aim to identify the areas with the less climatic stress for the species to adapt CC and envisage little or no habitat intervention. More realistic approaches assume not only the climatic regimes of areas along time but also evaluate the synergistic effects of climate and habitat condition, before and after a particular intervention is made, on species persistence. Under this scheme, not only the choice of protecting, or not, impacts the local environmental suitability for a species, but also specific management actions, taken locally (e.g., habitat restoration and conversion, land-use management, genetic fertilization, assisted colonization, etc.) influence environmental quality. These models define true dynamic problems, in which the future condition of areas is not predictable upfront but depends on the local or neighboring actions taken, up to a given time period. These are complex problems whose solution quality (i.e., optimality) rely on well-conducted simulation studies.

In dynamic models, varying the timing of an action may dictate quite different ecological benefits. Pressey et al. (2004) explored those impacts



New Paradigms for Modern Biogeography Conservation, Fig. 4 The concept of climate-adaptive trajectory for a species. (a) An index quantifying the persistence (P_C) of a species up to time period T_2 within the trajectory is obtained using local climatic suitability ($po_{..}$) and dispersal data ($pd_{..}$). $P_C = 0$ when a site within the trajectory is not suitable or when the species is unable to reach a site in the trajectory. The adaptive trajectories depart from sites where

the species is confirmed present (black cells); (b) example of adaptive trajectories for the Iberian Lynx from current time until 2080, under severe climate change. The “base map” refers to $po_{..}$ in current time; the “avg suitab map” refers to average $po_{..}$ across time, from current time to 2080; the “top ATs map” refers to the location of the 500 trajectories with the highest persistence scores (P_C)

by studying two conservation aptitudes based on action times. In the *minLoss* model, planners focus on vulnerable areas by minimizing the expected short-term biodiversity loss from the entire planning region. It assumes that low-vulnerability areas resemble short-term PAs. Under the *MaxGain* planners accept that habitat loss is uniformly distributed in the planning region and the areas with the highest biodiversity value are therefore targeted. When ongoing habitat loss occurs and habitat vulnerability is spatially high, *minLoss* outperforms *maxGain* in retaining biodiversity. The *maxGain* outperforms *minLoss* solutions under scenarios of uncertain funding or when areas with high biodiversity value and low short-term vulnerability cannot be scheduled for later protection (as assumed by *minLoss*). If vulnerability is overestimated, scarce resources can be directed to areas that do not require protection. Conversely, if vulnerability is underestimated, areas that are, in fact, threatened could be overlooked and have their conservation values reduced or extirpated. Using a badly informed *MinLoss* might therefore be worse than ignoring vulnerability altogether.

Socioeconomic Players

Up to the 1980s, the biodiversity conservation agenda was dominated by a philosophical context of putting great emphasis on the preservation of pristine habitats. More recently, social actions, needs, and expectations have been integrated in a holistic environmental overview that frames the modern concept of socioecological systems. Resilience of the whole socioecological system is nowadays a fully integrated idea, describing how nature and people absorb disturbance and maintain their function after important disturbances. With biodiversity becoming a very important asset in the global economy (through the concepts of ecosystem services), the backbone of global economic systems weights together societal, developmental, and ecological goals in the rhetoric of sustainability (Fig. 3).

Recent literature highlights the importance of incorporating socioeconomic costs into

conservation planning for two main reasons. First, including socioeconomic costs minimizes the impacts over resource users (Carwardine et al. 2008). Second, including those costs produces plans that are cost-effective to implement and manage (Naidoo et al. 2006). The inclusion of spatially explicit information on socio-economy in the planning process may reduce opportunity costs (the foregone revenue from other forms of space use), sometimes with no negative effects on the protection of conservation features. This should be implemented with caution because avoiding tensions and costly outputs may have negative ecological consequences, with the underrepresentation of biodiversity features when compared with socioeconomic-unconstrained conservation scenarios. In such cases, if there are requisites for specific biodiversity features, they need to be defined as strict solution requirements, to guarantee their adequate coverage even under integrative reconciliatory settings.

A central contribution of economists to the development of conservation plans involves the incorporation of financial costs into planning settings (Fig. 3). The inclusion of these costs in PA selection problems directs the efficiency assessment of plans to financial resources (i.e., budgets) rather than areal size or number of sites. When compared to standard area-based procedures, considering financial costs more clearly captures the conservation benefits to be obtained from the investments made and most likely generates distinct sets of optimal PAs (Ando et al. 1998). Socioeconomic costs associated to conservation include the capital needed: (1) for the acquisition of PAs (i.e., within land markets); (2) to establish time-limited contracts with landowners; (3) to compensate landowners for foregone revenues; and (4) to undertake conservation actions, which may depend, for example, on the distance to established PAs or to the operational headquarters of conservation organizations.

With explicit socioeconomic data available, a relevant problem to solve concerns the mutual optimization of conservation and socioeconomic revenues. In these multi-criteria settings, the maximization of ecological and socioeconomic revenues from PAs is made under distinct

arrangements. With the “minimum set cover” and the “maximal coverage” models (see above), the ecological and financial components of a plan are, respectively, fixed while the other is maximized. However, when a planner aims to achieve a fair compromise between the ecological and socio-economic goals, efficient frontiers (i.e., Pareto solutions) identify balanced solutions, in which the improvement of one side of the (socio-ecological) system implies the reduction on the revenues from the other side. By producing multiple “Pareto solutions” using distinct weighting schemes, planners have the chance to be informed on various options useful for the purpose of reconciling expectations of the socioeconomic and conservation players (Kurth et al. 2017).

Conservation actions are not only sources of lost financial aspects. In the last decade, a large emphasis of conservation planners has been put over the dual benefits of ecosystems services (see above). Apart from the ecological benefits of functional ecosystems, they also define financial revenues associated to functional habitats. This claims for a map of ecosystem service, not only on their natural units of measure but also using market (financial) currencies. Because these markets are not universal (both at the spatial extent and at the services they reflect) and because the scale of profits are typically wide-ranging, benefiting multiple players, a consensual conversion to monetary units is seldom possible (Mace et al. 2012).

Often, the financial costs of conservation decisions at local scale are not available. In these situations, approximated informers have been used instead. For example, the extent of PAs in each planning unit has been considered as an informer on the financial effort to put, because planning units with larger protected extents are, in principle, already owned by a conservation player and therefore acquisition costs are inexistent (e.g., Alagador et al. 2012). On the opposing side, levels of anthropic disturbance (e.g., using the Human Footprint Index, Sanderson et al. 2002) provide good guidance not only about disturbance regimes but also about the financial investment needed to acquire and restore lands. Araújo et al. (2008) used distance to urban centers

in Europe as a measure of threat that, like the previous one, positively correlates with the financial facet of conservation.

Conservation costs may also represent non-market values that impair conservation effectiveness (Chan et al. 2011); extinction risks associated to species occurring in each site (Game et al. 2008); and measurable uncertainties on local occurrences of species (Lemes and Loyola 2013).

Hard and Soft Land Ownership

Whereas targeted management of PAs is central for conservation of native biodiversity, there are portions of unprotected land that might play a significant role for gene flow, species dispersal, or species adaptation to CC. Although most of studies are largely biased in assuming conservation intervention solely based on land acquisition for PA establishment, in regions where a threat may be prevented with less strict measures or where lands are not exposed to numerous threats that cannot be tackled in a piecemeal manner, alternative policy mechanisms for off-PAs exist. While useful for protecting a few special areas of conservation interest, the upfront costs of acquiring land outright can be high when compared to other viable conservation approaches that may be carried out in private lands. An easement is a nonpossessory right to use the property of another legal person without changing its ownership. Private property subject to a conservation easement remains in private ownership, with only some of the use rights being restricted, in a way that furthers the goal of conservation either for perpetuity or a fixed period of time. The agreement may require landowners to take certain actions to protect the natural resources or to refrain certain actions, such as severe land transformation or land subdivision. The distinct modes these agreements impact local habitat and the socio-economy (land value) of the focal and neighboring lands may be introduced in the ecological and the socio-economic layers in analysis. As mentioned earlier, these types of feedbacks are well suited to be handled using true dynamic models.

Some of these agreements carry the additional obligation of landowners to promote biodiversity gains in some areas to be set against biodiversity losses in another (i.e., offsetting or compensatory regulations). The goal of biodiversity offsetting is to achieve no-net-loss and preferably a net gain of biodiversity with respect to species composition, habitat structure, and ecosystem function, cultural values associated with biodiversity, among others. This brings new questions for the design of conservation plans, because the identification of the “compensatory areas” may be seen as a scheduling problem per se (where, when, and what actions to undertake to a no-net-loss state is reached with the lowest investment?) or to be incorporated in broader conservation models (Gardner et al. 2013).

Spatially Explicit Data Challenges

A large suite of data needs to be considered when developing comprehensive conservation plans. Relevant data span from the independent distribution of several taxa and their inter-relationships (i.e., trophic interactions) to abiotic factors, threats, and socioeconomic layers. The larger the number of relevant processes analyzed, the more realistic models get. However, that comes at the expense of the time needed to undertake analyses and the ability of custom-solving algorithms to retrieve good quality (optimal) solutions. Faced with these drawbacks, planners need to consider the amount of data to analyze – the number of data layers (i.e., factors), the geographical extent and/or the geographical grain of analyses, the time periods to consider, and the number of biodiversity features and processes.

Many planners are captivated by the availability of high resolute data. However, they should consider that, although (spatially or temporally) more precise, those data may not be more accurate than coarse-resolute data, because the reality may be wrongly characterized under finer scales, if the concerning processes operate at broader scales. For example, *WorldClim* a portal that makes available bioclimatic data from several sources has available global data at 1 km-sq resolution.

These data result from statistical interpolation methods implemented homogeneously across large areas. The method overpasses topographic and water specificities that influence climatic patterns at local scale. Using these data as input for bioclimatic niche models, scale-related errors propagate resulting in over- or underrepresentation of suitable climatic regions for species. Furthermore, when calibrating bioclimatic niche models at, for example, 10 km-sq grain, projecting results at 1 km-sq may be counterproductive, even if climate data is accurate, because the magnitude and nature of response of a species at a given scale may not be replicated at a different one (e.g., at a coarse scale, temperature may be an important variable to take into consideration, but insolation, a variable that links to other topographic processes, may be most relevant at finer scales). This transition from broad-scale planning to fine-scale implementation has received little attention and should be fully acknowledged by planners.

In terms of geographic extent, the current environmental dynamics calls for geographic windows that go beyond the borders of focal areas. Potentially, some biodiversity features in the neighboring regions may enter the focal area in the near future and these impacts need to be anticipated. In the opposite side, potential trajectories of biodiversity leaving the focal regions may elicit communication and coordination with neighboring institutions such that the monitoring of a species is maintained. Because movements are seldom linear, “turning-back trajectories” are probable, especially in regions with large environmental heterogeneity and no clear geographic gradient of climate. The return of species needs to be anticipated to keep conservation resources prepared. The expansion of political, jurisdictional, and institutional scopes for effective biodiversity conservation profits not only from the individual potential of each player but, mainly, from collaborations and shared investments and benefits (Bladt et al. 2009).

Under modern conservation planning, the need to anticipate future trends requires that several time layers are used. Again, the availability of climate data and land-use models for the

upcoming decades under distinct climate storylines (Fig. 3) allows local suitability of species to be predicted, assuming that current and/or past relationships between species and climate and land uses are fixed along the time horizon under question. Although the implementation of conservation measures in place needs a certain degree of stability, the asynchrony between interventions in time and asynchrony between species responses may require that a relevant number of time periods in the future are assessed (e.g., annual data for 50 yrs. ahead). Again, this raises the problem of the curse of dimensionality which overarches the solvability of most spatially explicit problems in biogeography conservation.

The Way Forward

Researchers and planners are aware about the multiple factors that impinge biodiversity under nonlinear and complex forms, making the realized impacts larger than what could be predicted. Under the existing global crisis, with many habitats in poor condition and species threatened of extinction, calls have been made for the protection of 50% of terrestrial land by 2050. This will only be achievable with flexible and reconciliatory plans capable to unify biodiversity expectations with socioeconomic ones. The principles of “land sharing and land sparing,” that emerged to couple biodiversity conservation with agriculture production (Phalan et al. 2011), need to be extended to other land uses where some level of ecological value still exists.

Another consideration to attenuate conflicts passes by focusing conservation efforts in areas that go highly suitable for biodiversity and ecosystem services but that present low socioeconomic appeal (i.e., co-benefit areas). These “triple-win” areas may still need to be complemented with other areas where the ecological, service, and socioeconomic dimensions are balanced (multi-criteria optimization). These co-benefit areas should reflect a portfolio of options where trade-offs are established with varying weighting schemes for the distinct goals (i.e., distinct policies) (Gunton et al. 2017). For

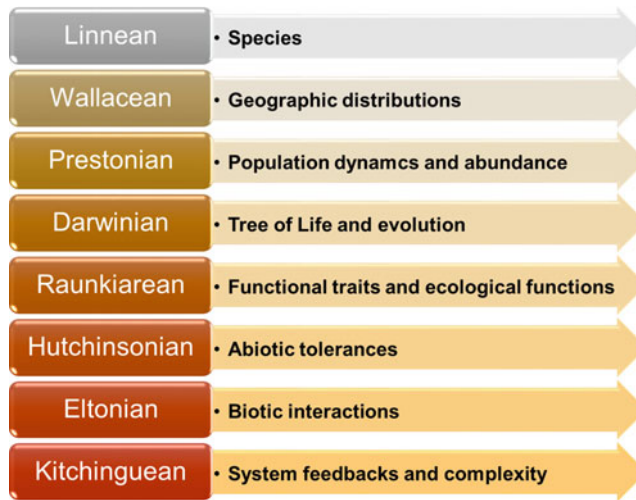
example, the recently launched European Green Deal calls for the reconciliation of nature-based climate mitigation, biodiversity conservation, and sustainable land-use policies, along the upcoming decades.

Looking upfront into the future, conservation plans buffer bio-socioeconomic systems from the negative impacts of implementing actions that at short term seem very encouraging but that, at long term, may result heavy detrimental. However, anticipative plans are naturally more susceptible to the uncertainties arising from spatial and temporal predictive exercises. Plans need therefore to explicitly integrate the measurable uncertainties and to provide redundant and robust options, using easy-adaptable and flexible instruments of adjustment to unforeseen scenarios. Under CC, where expectations of equilibrium are not met, PA managers need to take a long-term view, and act to promote species adaptation to CC. Plans should typically be conceived for periods up to 20 to 50 yrs., depending on the speed with which ecosystem changes are expected.

In the Age of Big Data, conservation planners have the opportunity to take control of their conservation systems. While shortening the major knowledge shortfalls still existing at several biogeographic scales (e.g., Linnean, Wallacean, Prestonian, Darwinian, Raunkiarean, Hutchinsonian, and Elthonian; Hortal et al. 2014) is a continuously demanding task, the planning of conservation investments in which many factors dynamically interact is likely to open a Pandora box of uncertainty regarding those complex systems (“Kitchingean” shortfall) that will feed further research (Fig. 5).

Final Remarks

The world is currently off course from achieving the Sustainable Development Goals (SDGs). No country is on track to achieve all of the SDGs, and progress is slowest on the environment-focused goals, such as the SDG 12 (responsible consumption and production), SDG 13 (climate action), SDG 14 (life below water), and the SDG 15 (life on land). Importantly, in order to fully embrace



New Paradigms for Modern Biogeography Conservation, Fig. 5 The shortfalls of biogeographic knowledge. The seven top ones are discussed in Hortal et al. (2014). The “Kitchingean” shortfall (following the work of R.L. Kitching on complex ecological systems) is herein

the SDG 15 goal, (1) biodiversity concerns need to be raised along hierarchical political structures worldwide (from international organizations to local communities); (2) biodiversity needs to be mainstreamed among political and socioeconomic sectors; (3) coherent and integrative policies accommodating distinct goals need to be established; (4) collaborative partnerships need to be encouraged, such that costs are split among the players and co-benefits upraised; and (5) using less strict protection actions may incentive the private sector to contribute for biodiversity condition while maintaining their customary land rights and financial outcomes.

Under the paradigm of biogeography, modern conservation planning requires much more than knowledge about the geography of ecological features. It also needs to integrate information on the current drivers of such patterns, by extending its boundaries out of the ecological world and foresee humans as niche constructors and destructors. Furthermore, effectiveness gains will emerge if opportunities to increase sociopolitical support are explored and if socioeconomic context and ecosystem services are fully integrated. This massive set of data needs to be appraised such that decision support maps respond to the “whats,” “wheres,” “whens,” and “hows” of conservation

introduced to characterize the difficulty of analyzing complex and dynamic systems and of making decisions related to a broad range of biodiversity elements and processes, across wide and fine resolute spaces, for many time periods

plans. The very active field of biogeography conservation has been giving a huge set of studies but seldom is carefully analyzed by governmental players (i.e., implementation gaps). This paradigm needs to change such that the SDG 15 and its interlinks with other SDGs are accomplished worldwide.

Cross-References

- ▶ [Biodiversity Erosion: Causes and Consequences](#)
- ▶ [Biodiversity Loss](#)
- ▶ [Biodiversity Loss and Countermeasures](#)
- ▶ [Conservation](#)
- ▶ [Human-Wildlife Conflict and Mitigation](#)
- ▶ [Land Use Intensity and Change: Impacts on Biodiversity](#)
- ▶ [Protected Areas](#)
- ▶ [Wildlife and Sustainable Development](#)

Acknowledgments This work was funded by National Funds through FCT – Portuguese Foundation for Science and Technology – under the Project UIDB/05183/2020 and by FEDER funds through COMPETE under the project PTDC/AAG-GLO/3979/2014 (ref. 9471-RIDTI).

References

- Alagador D, Cerdeira JO (2018) A quantitative analysis on the effects of critical factors limiting the effectiveness of species conservation in future-time. *Ecol Evol* 8 (6):3457–3467. <https://doi.org/10.1002/ece3.3788>
- Alagador D, Triviño M, Cerdeira J, Brás R, Cabeza M, Araújo M (2012) Linking like with like: optimising connectivity between environmentally-similar habitats. *Landscape Ecol* 27(2):291–301. <https://doi.org/10.1007/s10980-012-9704-9>
- Alagador D, Cerdeira JO, Araújo MB (2014) Shifting protected areas: scheduling spatial priorities under climate change. *J Appl Ecol* 51(3):703–713. <https://doi.org/10.1111/1365-2664.12230>
- Alagador D, Cerdeira JO, Araújo MB (2016) Climate change, species range shifts and dispersal corridors: an evaluation of spatial conservation models. *Methods Ecol Evol* 7(7):853–866. <https://doi.org/10.1111/2041-210x.12524>
- Anderson BJ, Akçakaya HR, Araújo MB, Fordham DA, Martinez-Meyer E, Thuiller W, Brook BW (2009) Dynamics of range margins for metapopulations under climate change. *Proc Roy Soc London B Biol Sci* 276(1661):1415–1420. <https://doi.org/10.1098/rspb.2008.1681>
- Ando A, Camm J, Polasky S, Solow A (1998) Species distributions, land values, and efficient conservation. *Science* 279(5359):2126–2128. <https://doi.org/10.1126/science.279.5359.2126>
- Araújo MB, Nogués-Bravo D, Reginster I, Rounsevell M, Whittaker RJ (2008) Exposure of European biodiversity to changes in human-induced pressures. *Environ Sci Pol* 11(1):38–45. <https://doi.org/10.1016/j.envsci.2007.07.002>
- Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. *Ecol Lett* 14:484–492. <https://doi.org/10.1111/j.1461-0248.2011.01610.x>
- Beier P, Sutcliffe P, Hjort J, Faith DP, Pressey RL, Albuquerque F (2015) A review of selection-based tests of abiotic surrogates for species representation. *Conserv Biol* 29(3):668–679. <https://doi.org/10.1111/cobi.12509>
- Bladt J, Strange N, Abildtrup J, Svenning J-C, Skov F (2009) Conservation efficiency of geopolitical coordination in the EU. *J Nat Conserv* 17(2):72–86. <https://doi.org/10.1016/j.jnc.2008.12.003>
- Bode M, Burrage K, Possingham HP (2008) Using complex network metrics to predict the persistence of metapopulations with asymmetric connectivity patterns. *Ecol Model* 214(2–4):201–209. <https://doi.org/10.1016/j.ecolmodel.2008.02.040>
- Brooks TM, Mittermeier RA, da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL (2006) Global biodiversity conservation priorities. *Science* 313(5783):58–61. <https://doi.org/10.1126/science.1127609>
- Carroll SP, Fox CW (2008) *Conservation biology: evolution in action*. Oxford University Press, Oxford, 380 pages
- Carvalho SB, Velo-Antón G, Tarroso P, Portela AP, Barata M, Carranza S, Moritz C, Possingham HP (2017) Spatial conservation prioritization of biodiversity spanning the evolutionary continuum. *Nature Ecol Evol* 1:0151. <https://doi.org/10.1038/s41559-017-0151>
- Carwardine J, Wilson KA, Watts M, Etter A, Klein CJ, Possingham HP (2008) Avoiding costly conservation mistakes: the importance of defining actions and costs in spatial priority setting. *PLoS One* 3(7):e2586. <https://doi.org/10.1371/journal.pone.0002586>
- CBD (2011) Conference of the Parties Decision X/2: Strategic plan for biodiversity 2011–2020
- Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC (2006) Conservation planning for ecosystem services. *PLoS Biol* 4(11):e379. <https://doi.org/10.1371/journal.pbio.0040379>
- Chan KMA, Hoshizaki L, Klinckenberg B (2011) Ecosystem services in conservation planning: targeted benefits vs. co-benefits or costs? *PLoS One* 6(9):e24378
- Chao A, Chiu C-H, Jost L (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. *Annu Rev Ecol Evol S* 45(1):297–324. <https://doi.org/10.1146/annurev-ecolsys-120213-091540>
- Cowling RM, Pressey RL (2001) Rapid plant diversification: planning for an evolutionary future. *PNAS* 98(10):5452–5457. <https://doi.org/10.1073/pnas.101093498>
- Decker E, Linke S, Hermoso V, Geist J (2017) Incorporating ecological functions in conservation decision making. *Ecol Evol* 7(20):8273–8281. <https://doi.org/10.1002/ece3.3353>
- Diniz-Filho J, Melo D, de Oliveira G, Collevatti R, Soares T, Nabout J, Lima J, Dobrovolski R, Chaves L, Naves R, Loyola R, Telles M (2012) Planning for optimal conservation of geographical genetic variability within species. *Conserv Genet* 13(4):1085–1093. <https://doi.org/10.1007/s10592-012-0356-8>
- Fordham DA, Akçakaya HR, Brook BW, Rodriguez A, Alves PC, Civantos E, Triviño M, Watts MJ, Araújo MB (2013) Adapted conservation measures are required to save the Iberian lynx in a changing climate. *Nature Clim Change* 3(10):899–903. <https://doi.org/10.1038/nclimate1954>
- Fuller RA, McDonald-Madden E, Wilson KA, Carwardine J, Grantham HS, Watson JEM, Klein CJ, Green DC, Possingham HP (2010) Replacing underperforming protected areas achieves better conservation outcomes. *Nature* 466(7304):365–367. <https://doi.org/10.1038/nature09180>
- Game ET, Watts ME, Wooldridge S, Possingham HP (2008) Planning for persistence in marine reserves: a question of catastrophic importance. *Ecol Appl* 18(3):670–680. <https://doi.org/10.1890/07-1027.1>

- Gardner TA, Von Hase A, Brownlie S, Ekstrom JMM, Pilgrim JD, Savy CE, Stephens RTT, Treweek JO, Ussher GT, Ward G, Ten Kate K (2013) Biodiversity offsets and the challenge of achieving no net loss. *Conserv Biol* 27(6):1254–1264. <https://doi.org/10.1111/cobi.12118>
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8(9):993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Guntton RM, Marsh CJ, Moulherat S, Malchow A-K, Bocedi G, Klenke RA, Kunin WE (2017) Multi-criterion trade-offs and synergies for spatial conservation planning. *J Appl Ecol* 54(3):903–913. <https://doi.org/10.1111/1365-2664.12803>
- Hannah L, Midgley GF, Lovejoy T, Bond WJ, Bush M, Lovett JC, Scott D, Woodward FI (2002) Conservation of biodiversity in a changing climate. *Conserv Biol* 16(1):264–268. <https://doi.org/10.1046/j.1523-1739.2002.00465.x>
- Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. *Nature* 404(6779):755–758. <https://doi.org/10.1038/35008063>
- Hortal J, de Bello F, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ (2014) Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu Rev Ecol Evol S* 46:523–549. <https://doi.org/10.1146/annurev-ecolsys-112414-054400>
- Iwamura T, Possingham HP, Chadès I, Minton C, Murray NJ, Rogers DI, Treml EA, Fuller RA (2013) Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *P R Soc London B Bio* 280(1761). <https://doi.org/10.1098/rspb.2013.0325>
- Johnston A, Auer T, Fink D, Strimas-Mackey M, Iliff M, Rosenberg KV, Brown S, Lanctot R, Rodewald AD, Kelling S (2020) Comparing abundance distributions and range maps in spatial conservation planning for migratory species. *Ecol Appl* 30(3):e02058. <https://doi.org/10.1002/eap.2058>
- Jones KR, Watson JEM, Possingham HP, Klein CJ (2016) Incorporating climate change into spatial conservation prioritisation: a review. *Biol Conserv* 194:121–130. <https://doi.org/10.1016/j.biocon.2015.12.008>
- Joppa LN, Pfaff A (2009) High and far: biases in the location of protected areas. *PLoS One* 4(12):e8273. <https://doi.org/10.1371/journal.pone.0008273>
- Kurth MH, Larkin S, Keisler JM, Linkov I (2017) Trends and applications of multi-criteria decision analysis: use in government agencies. *Environ Syst Dec* 37(2):134–143. <https://doi.org/10.1007/s10669-017-9644-7>
- Lefcheck JS, Bastazini VAG, Griffin JN (2015) Choosing and using multiple traits in functional diversity research. *Environ Conserv* 42(2):104–107. <https://doi.org/10.1017/S0376892914000307>
- Lemes P, Loyola RD (2013) Accommodating species climate-forced dispersal and uncertainties in spatial conservation planning. *PLoS One* 8(1):e54323. <https://doi.org/10.1371/journal.pone.0054323>
- Lorenzen ED, Nogués-Bravo D, Orlando L, Weinstock J, Binladen J, Marske KA, Ugan A, Borregaard MK, Gilbert MTP, Nielsen R, Ho SYW, Goebel T, Graf KE, Byers D, Stenderup JT, Rasmussen M, Campos PF, Leonard JA, Koepfli K-P, Froese D, Zazula G, Stafford TW, Aaris-Sørensen K, Batra P, Haywood AM, Singarayer JS, Valdes PJ, Boeskorov G, Burns JA, Davydov SP, Haile J, Jenkins DL, Kosintsev P, Kuznetsova T, Lai X, Martin LD, McDonald HG, Mol D, Meldgaard M, Munch K, Stephan E, Sablin M, Sommer RS, Sipko T, Scott E, Suchard MA, Tikhonov A, Willerslev R, Wayne RK, Cooper A, Hofreiter M, Sher A, Shapiro B, Rahbek C, Willerslev E (2011) Species-specific responses of late quaternary megafauna to climate and humans. *Nature* 479(7373):359–364. <https://doi.org/10.1038/nature10574>
- MacArthur RH, Wilson EO (2001) *The theory of island biogeography*. Princeton University Press, Princeton, 224 pages
- Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol Evolut* 27(1):24–31. <https://doi.org/10.1016/j.tree.2011.08.006>
- Margules CR, Pressey RL (2000) Systematic conservation planning. *Nature* 405(6783):243–253. <https://doi.org/10.1038/35012251>
- Midgley GF, Hannah L, Millar D, Thuiller W, Booth A (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Bio Conserv* 112(1–2):87–97. [https://doi.org/10.1016/S0006-3207\(02\)00414-7](https://doi.org/10.1016/S0006-3207(02)00414-7)
- Moritz C, Faith DP (1998) Comparative phylogeography and the identification of genetically divergent areas for conservation. *Mol Ecol* 7(4):419–429. <https://doi.org/10.1046/j.1365-294x.1998.00317.x>
- Naidoo R, Balmford A, Ferraro PJ, Polasky S, Ricketts TH, Rouget M (2006) Integrating economic costs into conservation planning. *Trends Ecol Evol* 21(12):681–687. <https://doi.org/10.1016/j.tree.2006.10.003>
- Ovaskainen O, Hanski I (2003) Extinction threshold in metapopulation models. *Ann Zool Fenn* 40(2):17
- Peters RL, Darling JDS (1985) The greenhouse-effect and nature reserves. *Bioscience* 35(11):707–717. <https://doi.org/10.2307/1310052>
- Phalan B, Onial M, Balmford A, Green RE (2011) Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333(6047):1289–1291. <https://doi.org/10.1126/science.1208742>
- Pressey RL, Watts ME, Barrett TW (2004) Is maximizing protection the same as minimizing loss? Efficiency and retention as alternative measures of the effectiveness of proposed reserves. *Ecol Lett* 7(11):1035–1046. <https://doi.org/10.1111/j.1461-0248.2004.00672.x>
- Redford KH, Adams W, Mace GM (2013) Synthetic biology and conservation of nature: wicked problems and wicked solutions. *PLoS Biol* 11(4):e1001530. <https://doi.org/10.1371/journal.pbio.1001530>

- Richardson DM, Whittaker RJ (2010) Conservation biogeography – foundations, concepts and challenges. *Divers Distrib* 16(3):313–320. <https://doi.org/10.1111/j.1472-4642.2010.00660.x>
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. *Bioscience* 52(10):891–904. [https://doi.org/10.1641/0006-3568\(2002\)052\[0891:thfatj\]2.0.co;2](https://doi.org/10.1641/0006-3568(2002)052[0891:thfatj]2.0.co;2)
- Thomassen HA, Fuller T, Buermann W, Milá B, Kieswetter CM, Jarrín-V P, Cameron SE, Mason E, Schweizer R, Schlunegger J, Chan J, Wang O, Peralvo M, Schneider CJ, Graham CH, Pollinger JP, Saatchi S, Wayne RK, Smith TB (2011) Mapping evolutionary process: a multi-taxa approach to conservation prioritization. *Evol Appl* 4:397–413. <https://doi.org/10.1111/j.1752-4571.2010.00172.x>
- WDPA (2020) Protected planet digital report. World Database Protected Areas. <https://livereport.protectedplanet.net/>. Accessed 1 Mar 2020
- Williams J, ReVelle C, Levin S (2005a) Spatial attributes and reserve design models: a review. *Environ Model Assess* 10(3):163–181. <https://doi.org/10.1007/s10666-005-9007-5>
- Williams P, Hannah L, Andelman S, Midgley G, Araujo M, Hughes G, Manne L, Martinez-Meyer E, Pearson R (2005b) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conserv Biol* 19(4):1063–1074. <https://doi.org/10.1111/j.1523-1739.2005.00080.x>
- Xu Y, Si Y, Takekawa J, Liu Q, Prins HHT, Yin S, Prosser D, Gong P, de Boer WF (2019) A network approach to prioritize conservation efforts for migratory birds. *Conserv Biol* 34(2):416–426. <https://doi.org/10.1111/cobi.13383>