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Review

Advances in systematic conservation planning to meet global biodiversity goals

Sylvaine Giakoumi ^{1,27,*}, Anthony J. Richardson^{2,3}, Aggeliki Doxa^{4,5}, Stefano Moro¹, Marco Andreello⁶, Jeffrey O. Hanson⁷, Virgilio Hermoso⁸, Tessa Mazor⁹, Jennifer McGowan², Heini Kujala¹⁰, Elizabeth Law¹¹, Jorge G. Álvarez-Romero^{12,13}, Rafael A. Magris¹⁴, Elena Gissi^{15,27}, Nur Arafeh-Dalmau^{2,16}, Anna Metaxas¹⁷, Elina A. Virtanen^{10,18}, Natalie C. Ban¹⁹, Robert M. Runya²⁰, Daniel C. Dunn², Simonetta Fraschetti^{21,27}, Ibon Galparsoro²², Robert J. Smith²³, Francois Bastardie²⁴, Vanessa Stelzenmüller²⁵, Hugh P. Possingham², and Stelios Katsanevakis²⁶

Systematic conservation planning (SCP) involves the cost-effective placement and application of management actions to achieve biodiversity conservation objectives. Given the political momentum for greater global nature protection, restoration, and improved management of natural resources articulated in the targets of the Global Biodiversity Framework, assessing the state-of-the-art of SCP is timely. Recent advances in SCP include faster and more exact algorithms and software, inclusion of ecosystem services and multiple facets of biodiversity (e.g., genetic diversity, functional diversity), climate-smart approaches, prioritizing multiple actions, and increased SCP accessibility through online tools. To promote the adoption of SCP by decision-makers, we provide recommendations for bridging the gap between SCP science and practice, such as standardizing the communication of planning uncertainty and capacity-building training courses.

Highlights

Systematic conservation planning (SCP) offers decision-makers an integrated approach to tackle multiple targets of international policies such as the Global Biodiversity Framework and, notably, to efficiently achieve the '30 × 30' target by protecting 30% of land and sea by 2030.

Recent advances in optimization tools have broadened the scope of problems that can be addressed by SCP. These include new and enhanced optimization methods and the integration of multiple objectives prioritizing actions across space and time.

Improved SCP methods and tools can assist decision-makers to better allocate resources. Building trust with decision-makers is crucial to reinforce the adoption of SCP for efficient biodiversity management.

Future SCP research could facilitate decision-makers in assessing trade-offs among conservation and socioeconomic objectives and estimating uncertainty in conservation plans.

The global need for systematic conservation planning

The Kunming–Montreal Global Biodiversity Framework (GBF) sets out the 2030 global agenda for nature conservation [1]. Under this framework, 196 countries have committed to protect 30% of the planet through an ecologically representative, well-connected, and equitably governed system of area-based conservation measures, as well as to restore 30% of degraded ecosystems (Targets 2 and 3). Spatial planning features prominently in the framework's Target 1: 'Ensure that all areas are under participatory, integrated, and biodiversity inclusive spatial planning and/or effective management processes'. Inherent within spatial planning is how decisions are made to allocate the use of limited resources in space and time, and it thus implicitly underpins almost every dimension of the GBF. The targets set by this framework are shaping national strategies for land, freshwater, and ocean protection as well as restoration and sustainable use of biodiversity. Decision-making in the next decade will have lasting effects on the planet and must be informed by spatial planning that is effective, robust, and transparent.

SCP offers a scientific process for improving spatial planning by identifying cost-effective conservation actions [2,3] (Box 1). With over three decades of applications worldwide, SCP has emerged as the leading approach to guide conservation investments [4]. The central steps within an SCP process include defining conservation objectives (e.g., maximizing biodiversity representation within protected areas), obtaining georeferenced data for **conservation features** (see Glossary) and socioeconomic activities, and then using mathematical algorithms to identify spatially explicit planning solutions ('prioritization') to guide the implementation of actions to

¹Department of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn, Sicily Marine Centre, Lungomare Cristoforo Colombo (complesso Roosevelt), 90149, Palermo, Italy

²School of the Environment and the Centre for Biodiversity and Conservation Science, University of Queensland, St Lucia, 4072, Queensland, Australia

³CSIRO Environment, St Lucia, 4067, Queensland, Australia

⁴Department of Ecology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki 54124, Greece

⁵Department of Ecology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki 54124, Greece

achieve the objectives [5,6]. Although many tools can play a role in guiding interventions for area-based conservation (including participatory Geographic Information System tools), here we focus on tools that attempt to optimize the prioritization of actions across large spatial extents for managing numerous and diverse conservation features, such as Marxan [7] and Zonation [8,9]. At their core, these **optimization tools** aim to address foundational SCP principles, including **comprehensiveness**, **adequacy**, **representativeness**, **efficiency**, and **connectivity** [10], which are reflected in the GBF. Ultimately, these principles aim to support the persistence of biodiversity while providing flexible planning solutions to decision-makers.

SCP tools, initially applied to design networks of protected areas, have recently expanded in number, scope, and complexity to assist in solving complex conservation problems. These next-generation SCP tools can consider multiple objectives; prioritize multiple actions; incorporate different types of connectivity, threats, and **costs**; and increase **stakeholder** engagement processes. A nonexhaustive list of free and open-source optimization tools indicates that they differ in the type of conservation challenges that they address, having different capabilities and attributes (Table 1). Although all these tools address SCP principles, their implementation varies, resulting in different prioritization outputs. For example, they may use distinct, explicit measures to assess the performance of solutions (termed ‘objective functions’). The use of different algorithms by different tools impacts both the runtime and the quality of planning solutions [11]. Moreover, some tools have been specifically customized to address particular challenges in SCP, including incorporating complex ecological processes such as connectivity (e.g., [12]).

We highlight recent advances in **spatial prioritization** made over the past 15 years, which have broadened the scope of problems addressable through SCP using optimization tools. We propose future research directions needed to fill critical gaps, such as designing dynamic planning solutions and improving the estimation of trade-offs when planning for multiple objectives (e.g., freshwater biodiversity conservation and securing water provision). Last, we explore and discuss strategies that could effectively bridge the gap between conservation planning science and practice.

Box 1. What is SCP?

SCP addresses the optimal spatial distribution and application of management actions to achieve conservation objectives [10,94]. SCP involves a goal-explicit, stagewise approach to allocating spatial conservation actions and devising management policies with feedback, potential revision, and reiteration at any stage [2,10]. Initially, the SCP framework included the following six steps [2]: (i) gathering information on biodiversity for the focal region; (ii) identifying conservation objectives (quantitative targets for species, habitats, and design attributes such as connectivity); (iii) reviewing existing conservation areas to assess the extent to which quantitative targets are achieved by existing protection; (iv) selecting additional conservation areas (identify potential new conservation areas to complement existing ones; this step is known as ‘spatial prioritization’); (v) implementing conservation actions (deciding on the most appropriate or feasible management for each area); and (vi) maintaining the required values of conservation areas by monitoring and adaptive management. This initial framework was further developed to include social dimensions more explicitly as separate steps in the framework, including stakeholder engagement to incorporate values from various stakeholders within a transparent and inclusive process and the collection of data on socioeconomic activities and anthropogenic threats to biodiversity in the focal region [3] (Figure 1A).

SCP has traditionally been applied to design networks of conservation areas to promote the persistence of biodiversity and other natural features. Using a variety of sophisticated mathematical algorithms and optimization tools, SCP identifies areas that maximize the representation of conservation features within budgetary limits or achieve the representation objectives (targets) while minimizing the cost associated with protection. A fundamental characteristic of SCP tools is that they identify complementary areas that collectively achieve the required objectives [95] (Figure 1B). The use of such optimization methods and tools represents a major improvement over previous additive scoring approaches incapable of addressing the fundamental concepts of SCP or tackling the need to design efficient networks of complementary conservation areas.

⁵Department of Biology, University of Crete, University Campus Vouton, 70013 Heraklion, Greece

⁶Institute for the Study of Anthropogenic Impacts and Sustainability in the Marine Environment, National Research Council, Via Della Vasca Navale 79, 00146, Rome, Italy

⁷Department of Biology, Carleton University, K1S 5B6 Ottawa, Ontario, Canada

⁸Departamento de Biología de la Conservación y Cambio Global, Estación Biológica de Doñana – CSIC, Americo Vespucio 26, 41092 Seville, Spain

⁹Biodiversity Division, Department of Energy, Environment, and Climate Action, 3002, East Melbourne, Victoria, Australia

¹⁰Finnish Natural History Museum, University of Helsinki, P.O. Box, FI-00014, Helsinki, Finland

¹¹Working Conservation Consulting, Fernie, V0B 1M0, British Columbia, Canada

¹²Global Science, The Nature Conservancy, Hobart, 7004, Tasmania, Australia

¹³Marine Biology and Aquaculture, James Cook University, Townsville, 4810, Queensland, Australia

¹⁴Chico Mendes Institute for Biodiversity Conservation, Brazilian Ministry of the Environment and Climate Change, EQSW 103/104, 70670-350, Brasília, / DF, Brazil

¹⁵Institute of Marine Sciences, National Research Council, Arsenale, Tesa 104 – Castello 2737/F, 30122, Venice, Italy

¹⁶Oceans Department, Hopkins Marine Station and Center for Ocean Solutions, Stanford University, Pacific Grove, CA, 93950, USA

¹⁷Department of Oceanography, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4R2, Canada

¹⁸Finnish Environment Institute, Nature Solutions (Marine Ecology), Latokartanonkaari 11, 00790, Helsinki, Finland

¹⁹School of Environmental Studies, University of Victoria, Victoria, British Columbia V8P 3E6, Canada

²⁰Fisheries Ecosystems Advisory Services (FEAS), Marine Institute, Galway, H91 R673, Ireland

²¹Department of Biology, University of Naples Federico II, Naples, 80126, Italy

²²AZTI, Marine Research, Basque Research, and Technology Alliance (BRTA), Herrera Kaia, Portualdea z/g, Pasaia 20110, Spain

²³Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, Kent CT2 7NR, UK

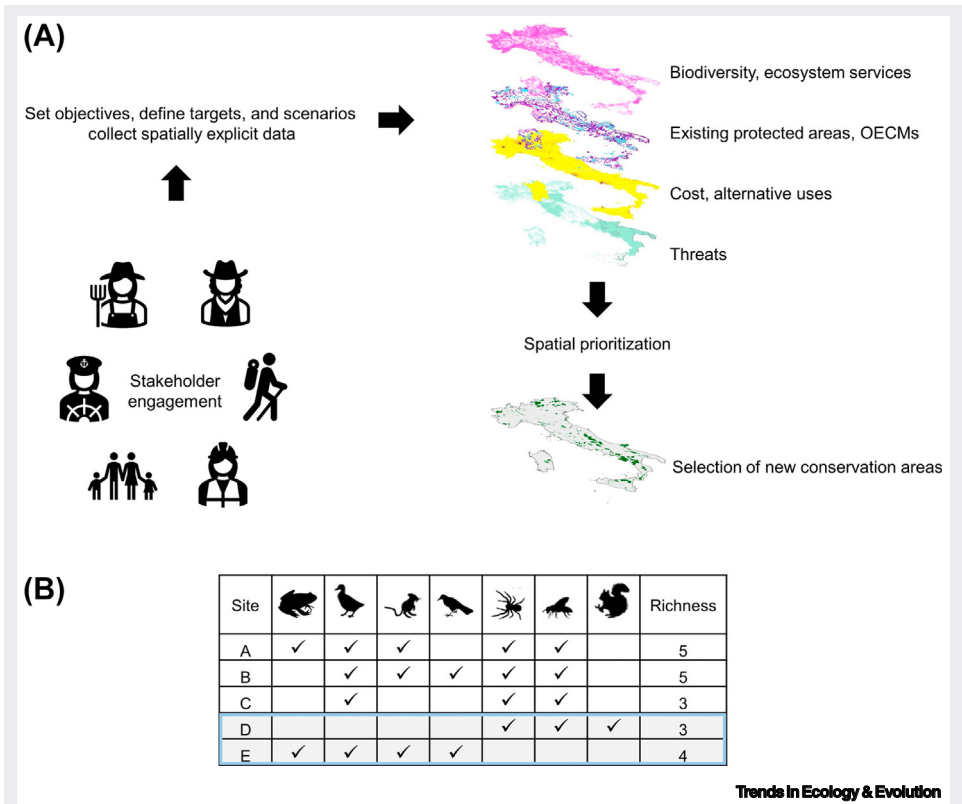


Figure 1. Graphical representation of the main steps in the systematic conservation planning (SCP) framework (A) and the principle of complementarity (B). Conservation planners, after setting conservation objectives and defining quantitative targets for conservation features (e.g., species and ecosystems of conservation interest) with stakeholders (e.g., farmer associations and hiking organizations), collect spatial data on biodiversity, socioeconomic uses, and existing managed areas (protected areas and other effective area-based conservation measures). Then, through spatial prioritization using optimization tools, they identify new conservation areas in which conservation measures can be implemented, monitored, and adaptively managed. New areas are selected on the basis of the principle of complementarity. In this example, although species richness is higher in planning sites A and B, the more efficient (cheaper) solution that protects all species is D and E. This logic underpins all systematic conservation plans. Abbreviation: OECMs, other effective area-based conservation measures.

Recent advances in SCP concepts, tools, and approaches

A summary of the major advances in SCP and spatial prioritization over the past 15 years, along with their outcomes, is shown in Figure 1. This diverse range of primary recent advances in optimization tools and spatial prioritization has been grouped in the following subsections.

Expanding methods to solve optimization problems

Some SCP tools, such as Marxan and Zonation, use metaheuristic algorithms together with a mathematically defined objective to generate prioritizations for finding near-optimal solutions. Metaheuristics are strategies that guide the search process to explore the search space efficiently. While they do not guarantee the identification of a single optimal solution, they can achieve near optimality and are well-suited for large, mathematically complex, and nonlinear optimization problems [8]. This nonlinearity allows consideration of aspects such as functional connectivity and species area-based extinction risk. More recently, there has been rapid progress in the development of exact algorithms that are mathematically guaranteed to identify optimal solutions [11,13]. For example, the *prioritizr* and *prioriactions* R packages employ mixed

²⁴Technical University of Denmark, Lyngby, 2800, Denmark

²⁵Thünen Institute of Sea Fisheries, Bremerhaven, 27572, Germany

²⁶Department of Marine Sciences, University of the Aegean, Mytilene, 81100, Greece

²⁷NBFC, National Biodiversity Future Center, Palermo, Italy

*Correspondence: sylvaine.giakoumi@szn.it (S. Giakoumi).

integer programming solvers to find the optimal solution. Exact algorithms are generally faster than metaheuristics when solving linear or quadratic conservation planning problems [11,13,14]. Newer approaches harnessing artificial intelligence (AI) technology include the tool CAPTAIN [15], which combines individual-based simulations with AI to identify spatial priorities for conservation according to user-defined targets. However, the ability of AI to solve a range of conservation problems remains to be tested.

Capturing additional facets of biodiversity and ecosystem services

Traditionally, SCP applications have been focused on representing species and ecosystem distributions within proposed protected area systems. Recently, the scope of SCP has broadened to incorporate other facets of biodiversity, such as intraspecific genetic diversity for long-term species persistence [16–18], functional diversity [19,20], and phylogenetic diversity (or diversity of evolutionary histories [21]). Moreover, recent advances in the sequencing technologies of environmental DNA have allowed SCP studies to generate more comprehensive solutions by providing information on the distribution of taxa that are usually undetected by visual surveys [22]. Capturing better and more aspects of biodiversity in SCP is important for identifying more representative, comprehensive, connected, and adequate protected area networks that can secure species persistence and maintenance of ecological functions. This need is also reflected in the GBF's Target 4, where the maintenance and restoration of genetic diversity through conservation actions is explicitly stated.

Furthermore, more studies in the past decade have incorporated benefits of ecosystem services in SCP, including coastal protection; water provision; and agricultural, fisheries, and forestry production [23–25]. These theoretical and methodological advances have allowed planners and conservation practitioners to incorporate missing ecological, socioeconomic, and policy considerations critical to inclusive, equitable, and effective area-based conservation interventions [23].

Prioritizing conservation actions and multiobjective planning

A key conceptual advance in SCP has been the shift toward prioritizing conservation actions in space and time over only identifying areas to protect. This approach recognizes that tangible outcomes and costs are associated with specific actions, rather than with species, locations, or threats [6]. For example, prioritizing land-use practices outside protected areas can be an efficient complementary strategy to reduce biodiversity loss [26]. Moreover, a recent development in SCP has been multiaction prioritization, which considers the contribution of various land- or sea-use types toward conservation and societal objectives (e.g., [27,28]). Multiobjective and multizoning planning allows us to solve more complex conservation problems that generate both biodiversity and socioeconomic outcomes with the potential to contribute to GBF's Target 10 ('Enhance biodiversity and sustainability in agriculture, aquaculture, fisheries, and forestry'). For example, Law *et al.* [28], used Marxan with Zones to compare different policy scenarios, setting objectives for forest protection, restoration, and rural development in Indonesia, and highlighted the trade-off between oil palm and smallholder agriculture, subject to the achievement of a set of carbon, timber, and biodiversity **conservation targets**. Newer tools with greater functionality have also been designed (e.g., the *priori*actions R package [29]). These new tools allow the use of more than one cost metric or threat type. Tools that prioritize multiple concurrent actions can also be used for optimizing both restoration and protection initiatives (e.g., [30]), whereas the *restopt*r R package [31] was specifically designed to inform restoration planning.

Addressing multiple types of connectivity

A critical aspect and challenge in SCP tool development is integrating various forms of connectivity, from populations to ecosystems [32]. Different species and habitats exhibit unique connectivity

Glossary

Adequacy: an adequate system of conservation areas should be large enough to ensure the persistence of each ecosystem and species.

Climate refugia: areas where climate is projected to remain relatively stable or where climate may stay suitable for a species.

Comprehensiveness: a comprehensive system of conservation areas is one that samples the main components of biodiversity within a region of interest (e.g., ecoregions, habitat types, or species).

Connectivity: a connected system of conservation areas ensures the flow of materials, including energy, organisms, and/or genes, among habitat patches, ecosystems, or regions of interest. Movement of these agents can be facilitated through the physical arrangement of physical structures (structural connectivity) and/or according to the capacity of agents to respond to physical structures (functional connectivity).

Conservation areas: places where some form of spatially explicit management is undertaken to contribute to conservation objectives; two prominent broad types are protected areas and other effective area-based conservation measures.

Conservation features: these are targeted by conservation efforts and include the presence or distribution of a species, habitat, or other elements of conservation importance such as ecological processes and social, economic, cultural, or spiritual values considered in plans.

Conservation target: the minimum amount of a conservation feature to be conserved, restored, or managed, often expressed as a percentage of the total amount of the conservation feature within a planning region.

Cost: social, economic, political, or cultural constraints associated with conservation actions such as costs related to acquisition (e.g., cost of buying land), management (e.g., enforcement and implementing costs of protected areas), transactions (e.g., costs associated with negotiating protection), opportunity cost (i.e., estimates of foregone revenues or economic livelihoods from protecting an area), or cultural cost (e.g., estimates of loss in cultural or spiritual value).

Efficiency: a cost-efficient system of conservation areas is one that

patterns, which complicate the prioritization problem. Tools and methods for incorporating connectivity within conservation problems have expanded [12] both in terms of their ability to address structural connectivity (e.g., via increasing clumping using neighbor constraints or border minimization) and also for the more complex functional connectivity for species-specific dispersal capability and directional flows (e.g., via optimizing metrics informed by connectivity data or considering spatial dependencies among sites). When accounting for connectivity, the best approach to pursue will depend on factors specific to the particular planning context, including the management objectives, the rate of disturbance outside selected areas, and the availability of connectivity information [e.g., 33].

Furthermore, it has become clear that the spatial planning process sometimes needs to extend beyond the initial place of interest to manage elements such as upstream nutrient and sediment runoff, essential for protecting interconnected land, freshwater, and marine ecosystems. Multirealm SCP [34,35] has led to innovative methods for identifying priority areas for cross-realm connectivity in species movements and human threats [36,37]. While current methods to account for connectivity present challenges for exact algorithms because these methods massively increase problem size and complexity, metaheuristics can incorporate species-specific dispersal capability into large-scale prioritization problems [38].

Climate-smart conservation planning

Besides developing tools that facilitate solving complex problems, conservation planners are increasingly suggesting approaches to account for climate change impacts on biodiversity when prioritizing areas and actions. Such approaches include protecting **climate refugia**, choosing areas highly resilient to climate impacts, selecting areas with a range of different climate exposures, and maintaining connectivity under future climate scenarios [39–41]. Methods for identifying climate refugia and integrating climate metrics and scenarios into SCP tools consider both species-dependent and -independent climate metrics [42–44] and project ecological processes [45,46]. Including changes in ecological processes is critical to ensure the functioning of protected area networks under present and future climates. For example, it is a priority to identify and protect critical network nodes under different climate scenarios because climate change impacts bird migration patterns [47] and marine larvae [48], often limiting their dispersal capacity and isolating some nodes of the network [46,49]. Historical data for identifying climate-resilient areas, microclimates, have been used to map climate refugia [40]; however, we need to better understand how these refugia reflect species-specific ecological responses, adaptation, and human responses to climatic changes.

Moreover, incorporating climate change and biodiversity over thousands of meters of ocean depth into marine planning has provided new approaches using different tools (Marxan [50], *prioritizr* [51], Zonation [52]) that can be applied to underpin the establishment of protected areas into the high seas beyond national jurisdictions. Addressing the climate-induced compression of 3D habitats, particularly through constraints on vertical or altitudinal migration or the connection between surface and groundwater systems, is critical for identifying and protecting sites that ensure spatial coherence and facilitate the multidimensional redistribution of biodiversity [53–55].

Increasing SCP tool accessibility

Recent efforts of the scientific community have also been extended to ensure meaningful stakeholder participation by making SCP tools and methods more accessible and interpretable to non-experts. Such efforts are important for mainstreaming SCP considerations into policy and effectively scaling spatial planning to reach conservation targets. Successful SCP stories demonstrate that stakeholders should be engaged from the outset [56]. Increased tool accessibility has

maximizes the conservation benefits per unit cost or minimizes opportunity cost and negative impacts on stakeholders associated with conservation.

Optimization tools: software used for defining, modeling, and solving conservation problems using mathematical algorithms.

Pareto frontiers: any point on a Pareto frontier represents optimal trade-offs among objectives.

Representativeness (or representativity): a representative system of conservation areas is one that includes a representative sample of all biodiversity present in a region, taking into account composition (e.g., species and genetic diversity), structure (e.g., habitat types), and function (e.g., recruitment and dispersal processes).

Spatial (conservation) prioritization: the allocation of effort and funds in space and time to achieve conservation objectives. It includes the identification of permanent or temporary spatial priorities for implementing conservation measures and scheduling the implementation of these measures through time; it also includes identifying priorities for the allocation of habitat restoration and biodiversity offsetting in different periods.

Stakeholders: people, organizations, or entities (e.g., governing institutions, resource users, experts) who will affect or be affected by conservation actions or contribute to the planning process. They include rights-holders and other interested parties, including industries such as agriculture, energy, fisheries, forestry, mining, and tourism.

Table 1. Main free and emerging open-source tools for systematic conservation planning

Optimization tool	Problem formulation	Refs	Problem type		Software attributes		
			Prioritization of a single action ^a	Prioritization of multiple actions ^b	Format	Community of practice	Algorithm
Marxan https://marxansolutions.org/software/	Uses minimum set formulation to identify the 'cheapest' set of planning units ^c for implementing management actions while ensuring each conservation feature meets a representation target	[7]	✓	– ^d	Desktop application, online web application	Google group (https://groups.google.com/g/marxan), Marxan Solutions (marxansolutions.org)	Heuristic/metaheuristic algorithms: flexible in finding near-optimal solutions to nonlinear conservation problems with increased complexity
Marxan with connectivity/ Marxan Connect https://marxansolutions.org/software/ https://marxanconnect.ca	Uses same problem formulation as Marxan but allows for more sophisticated connectivity	[12]	✓	–	Desktop application	Google group (https://groups.google.com/g/marxan), Marxan Solutions (marxansolutions.org), https://marxanconnect.ca	
Marxan with probabilities https://marxansolutions.org/software/	Similar to Marxan but includes additional objective function term specifying future probability of a site being destroyed. Helps plan for persistence in protected area networks.	[90]	✓	–	Desktop application	Google group (https://groups.google.com/g/marxan), Marxan Solutions (marxansolutions.org)	
Marxan with Zones https://marxansolutions.org/software/	Incorporates multiple costs and zones. Assigns each planning unit to a zone to meet ecological, social, and economic objectives at minimum cost.	[91]	✓	✓	Desktop application	Google group (https://groups.google.com/g/marxan), Marxan Solutions (marxansolutions.org)	
Zonation https://zonationteam.github.io/Zonation5/	For a conservation action (protection, restoration, management), it iteratively sorts all planning units until it finds a rank order that maximizes marginal gains to biodiversity features per area or budget used.	[9]	✓	–	Desktop app or via command line	Git-Hub (https://github.com/zonationteam/Zonation5)	

Prioritizr https://prioritizr.net/	A flexible tool for building and solving systematic conservation planning problems. Includes a variety of objectives (e.g., minimum set and budget-limited formulations), constraints, penalties, and decision types.	[92]	✓	✓	R package	GitHub (https://github.com/prioritizr/prioritizr/issues)	Exact algorithms: guaranteed to find optimal (or near-optimal within a prespecified optimality gap) solutions to linear conservation problems. Uses external solvers based on mixed integer or constant programming techniques.
Prioriactions https://prioriactions.github.io/prioriactions/	Solves multi-action threat management planning problem. Involves selecting (i) sites and (ii) actions at sites to address threats against species.	[29]	–	✓	R package	GitHub (https://github.com/prioriactions/prioriactions/issues)	
Coco https://github.com/esvanmantgem/coco	Designs ecologically connected conservation networks, directly optimizing connectivity metrics	[14]	✓	–	Python module	GitHub (https://github.com/esvanmantgem/coco)	
Restoptr https://github.com/dimitri-justeau/restoptr	Identifies priority areas for restoration by maximizing landscape indices. Constraints ensure priority areas exhibit particular characteristics (e.g., priority areas form a single contiguous network).	[31]	✓	–	R package	GitHub (https://github.com/dimitri-justeau/restoptr)	
CAPTAIN https://github.com/captain-project/captain-project	Optimizes conservation policy within constraints of a limited budget and a specific policy objective, such as minimization of species loss or maximization of protected area	[15]	✓	–	Python module, desktop application coming	GitHub (https://github.com/captain-project/captain-project/issues)	AI – reinforcement learning algorithm. Identifies optimal solutions while maintaining flexibility. Warrants assessment of its capacities and limitations in solving complex conservation problems.

^aFor example, prioritize areas for protection or restoration; identify priority areas for invasive species eradication or dam removal.

^bFor example, prioritize areas for protection and restoration; identify priority areas for invasive species eradication and dam removal and wetland protection.

^cPlanning units: natural, administrative, or arbitrary subdivisions of planning domains used for assessment and as building blocks for systems of conservation areas.

^dNot suitable.

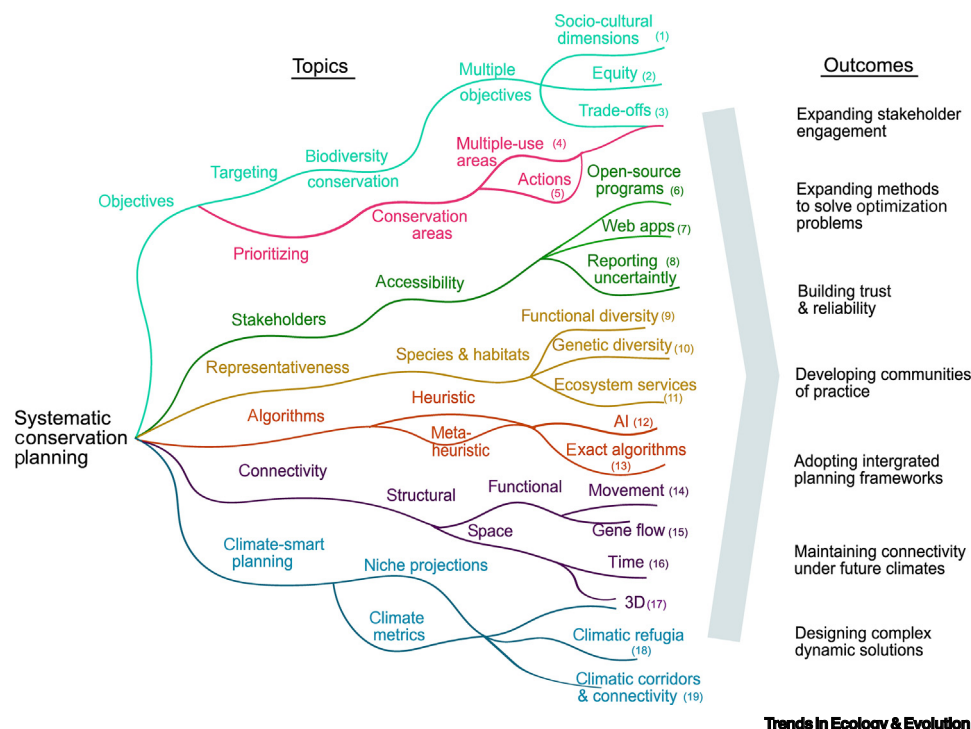


Figure 1. Advances in systematic conservation planning (SCP) concepts and methods addressing critical spatial prioritization topics (left) linked to key outcomes (right). The left part of the figure represents a rough timeline rather than a logical evolution of methods/concepts. For example, exact mathematical models are not an evolution of heuristics or metaheuristics, but they started being commonly used later. Seminal articles or recent reviews on the topics are reported: (1) Iwamura *et al.* [84], (2) Law *et al.* [78], (3) Halpern *et al.* [79], (4) Jung *et al.* [76], (5) Tallis *et al.* [6], (6) Moilanen *et al.* [9], (7) Marxan Planning Platform (<https://marxanplanning.org>), (8) Kujala *et al.* [69], (9) Pollock *et al.* [19], (10) Carvalho *et al.* [16], (11) Villarreal-Rosas *et al.* [23], (12) Silvestro *et al.* [15], (13) Beyer *et al.* [11], (14) Beger *et al.* [32], (15) Nielsen *et al.* [18], (16) Hermoso *et al.* [93], (17) Venegas-Li *et al.* [50], (18) Carroll *et al.* [39], and (19) Lawler *et al.* [42]. Abbreviation: AI, artificial intelligence.

been made possible via the creation of web applications that provide user-friendly interfaces for practitioners (e.g., Marxan Planning Platform; <https://marxanplanning.org>; Where to Work, <https://ncc.carleton.ca/>). Web applications provide several advantages, including (i) infrastructure for performing computational analyses, removing the need for high-performance computing; (ii) access to tools across a variety of operating systems; (iii) less expertise and time required to establish complex workflows; (iv) data storage and sharing; and (v) rapid access to the latest updated software version. Most important, these applications can facilitate collaboration and learning and enhance trust, legitimacy, and ownership of planning outputs, which are essential elements for the successful implementation of conservation actions. Like with every tool, a potential disadvantage is its incorrect use by nonexperts. To avoid such cases, increased capacity building is required.

Future research directions

Despite the significant recent advances, SCP tools and methods still face limitations and gaps that warrant further development. Based on our collective expertise, we recommend focusing future research on the following topics.

Designing dynamic planning solutions

Most SCP tools cannot directly provide dynamic solutions, since they do not explicitly incorporate planning over time. While it is possible to include dynamic threats by sequentially applying static

approaches incorporating multiple time steps in one prioritization [57,58] or zoning scheme, where each time frame is addressed through an independent zone [59,60], these approaches often fail to consider the time dependency of decisions and how delaying actions can impact conservation features. In marine conservation planning, coupled spatial solutions provided by SCP tools and system dynamics models aimed to generate dynamic solutions (e.g., [61]). However, this coupling of tools has disadvantages, including increased demand of data and uncertainty and limited accessibility to nonexperts.

Future tool development in SCP could focus on explicitly integrating the dynamics of both biodiversity features and their threats into a single planning tool. Such integration would enable the efficient sequencing of management actions in response to dynamic and emerging threats, budget availability, and changing environments [62]. Further efforts are needed to address the stochasticity associated with these dynamic problems (e.g., uncertainty regarding when or where threats could appear) and to understand the potential utility of dynamic protected areas, temporal transitions, and their inclusion in SCP. This will require innovative optimization algorithms to manage the complexity of dynamic problems. Networks of static and dynamic protected areas both on land and in the ocean could qualify as area-based management tools with the potential to significantly improve conservation outcomes [63,64].

Improving climate-smart planning

In instances when climate change has been addressed in conservation planning, it has typically only been included in a limited portion of the SCP process. However, climate-smart planning should infuse climate change considerations into all aspects of conservation planning by (i) setting climate adaptation objectives and targets, (ii) developing spatial layers that align with these objectives, (iii) evaluating alternative climate scenarios and their outcomes, (iv) refining climate adaptation objectives and targets, and (v) prioritizing climate-smart areas [46,55].

Climate-smart planning is often hindered by the lack of clear objectives and an uncertain theory of change (i.e., a comprehensive description and illustration of how and why a desired change is expected to happen in a particular context). For instance, many different climate-smart approaches are used in prioritizations: selecting climate refugia [52], preferentially selecting adaptation hotspots where there are likely to be genotypes more resilient to climate change [65], and choosing climate-representative areas where protected areas are placed across a range of climate futures [66]. The strengths, weaknesses, and efficacy of these various approaches is unknown. A stronger theory of change linking climate change impact on species to conservation outcomes is needed. This in turn could inform clearer climate-smart objectives.

Estimating and reporting uncertainty

While SCP tools can handle data uncertainty, they often underreport the uncertainty introduced by input data and user decisions [67–69]. In real-world applications, errors in species distribution models can significantly impact spatial prioritization [70]; yet, these errors are rarely quantified or considered (Box 2). Careful consideration should also be given to the uncertainty related to socioeconomic data included in spatial prioritization (either as costs or as threats to biodiversity), because they can profoundly affect conservation priorities [71,72]. Socioeconomic data associated with land values can undergo rapid changes [71], while the availability of cost data is very limited in the marine realm and surrogates are often used [72]. Greater use of sensitivity analyses is needed to assess how uncertainties in spatial data and the incorporation of new information, such as the inclusion of additional conservation features or spatial distribution data covering different time periods, could modify total conservation costs and the overall SCP outcomes [69,73].

Box 2. Uncertainty in species distribution modeling and SCP

Spatial prioritization outputs are only as robust as the data that underpin them. Spatial information on species is often produced from species distribution models (SDMs). Major sources of uncertainty in SDMs stem from model selection and parameterization [96]. In addition, when presence-only data are available, SDMs are estimated by generating pseudoabsences, introducing a scale-dependent bias that cannot be easily controlled [97,98]. Presence-only data are common in large biodiversity repositories (e.g., the Global Biodiversity Information Facility - GBIF and the Ocean Biogeographical Information System - OBIS). Uncertainties in SDMs can lead to misplaced conservation efforts and more expensive plans through the neglect of areas erroneously deemed as unimportant (omission errors) or the allocation of resources to areas with little conservation value (commission errors).

Errors in SDMs can be mitigated by careful model building in terms of parameters, appropriate validation techniques (e.g., the use of field data to refine and improve model accuracy), and improved modeling methods. For example, point process models have been proposed as the most natural way to analyze presence-only data, addressing scale-dependent biases and accounting for sampling biases [98]. Particularly in the Bayesian framework [99], point process models can enable real integrated distribution modeling, which allows harmonization of various data sources within a single modeling exercise while mitigating different sampling biases [100].

SCP tools could also benefit from better handling of uncertainty associated with SDMs. One approach is to discount areas with higher uncertainty [101]. Another is to find solutions that meet predefined objectives without regard to data uncertainties. By considering SDM uncertainty within the SCP framework, the resilience and adaptability of conservation plans to changing conditions and uncertainties in species distributions could be enhanced (see Figure I highlighting uncertainties associated with the distribution of the white shark in the Mediterranean Sea). However, the effect of SDM uncertainty on SCP results is nonlinear; sometimes, changes in the spatial patterns of species will not alter significantly the prioritization result (e.g., [69]). Better understanding of this relationship would enable us to identify when resolving uncertainties is important for developing effective prioritizations (e.g., [102]).

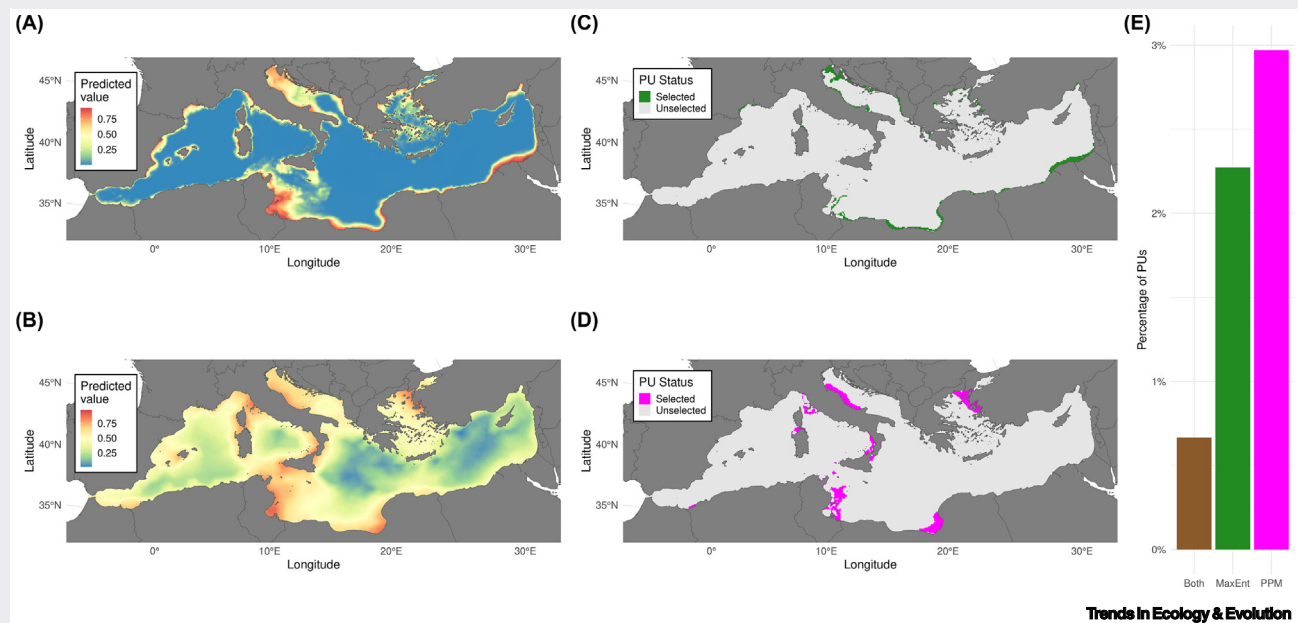


Figure I. The distribution of white shark (*Carcharodon carcharias*) based on two different species distribution models (SDMs) and the contrasting subsequent priority conservation area selections in the Mediterranean Sea. This simplistic example illustrates how the selection of different SDMs can lead to different prioritization plans for achieving the same conservation targets when environmental parameters used in SDMs and cost data used in systematic conservation planning (SCP) are kept constant. The species modeled distribution is based on estimates using (A) Maximum Entropy (MaxEnt) with the default settings and (B) a point process model in a Bayesian framework. The same data and covariates were used [103], and intensity values were scaled between 0 and 1. Also, the same cost distribution data were used [72]. Maps illustrating the priority areas selected by the prioritizr R package to conserve 60% of the species distribution across the Mediterranean Sea using the distributions based on (C) MaxEnt and (D) the point process model. In both cases, the threshold of 0.7 was set to define the presence of a species in a planning unit (PU) (each planning unit represents a discrete locality in the study area that can be managed independently of other areas). The bar plot (E) presents the percentage of selected planning units in (C) only (in green), in (D) only (in magenta), and in both prioritizations (in brown).

Beyond sensitivity analysis of conservation features, their targets, and cost metrics, adopting futures thinking and scenario analysis considering alternative pathways and trends of critical drivers of social-ecological systems (e.g., ecological, political, technological, and economic) could assist decision makers to better deal with uncertainty [74]. Scenario analysis could be

used to create different plans for alternative futures, with the aim of handling uncertainty and maximizing the probability of achieving conservation outcomes. A well-established financial framework, Modern Portfolio Theory, constructs and selects optimal asset allocation strategies for a given level of risk and has recently been adapted to address uncertainties in conservation planning related to climate change [75]. This approach highlights the potential of integrating theories from research fields accustomed to high uncertainty (such as finance) into SCP for enhancing conservation decision-making under uncertainty.

Dealing with trade-offs

Conservation planners must balance trade-offs associated with the increasing complexity in SCP, such as accounting for multiple current and future uses (e.g., land conversion for agriculture, renewable energy, and urbanization), including ecosystem services (e.g., food production), and climate change simultaneously. This means that the raft of potentially competing objectives increases and SCP algorithms need to wrangle multiple objectives equitably (e.g., [76,77]). Balancing such trade-offs is nontrivial, and previous work has suggested **Pareto frontiers** to estimate trade-offs among policy scenarios that aim at achieving socioeconomic and conservation objectives (e.g., [28]). Although existing SCP tools (e.g., Marxan with Zones) can estimate trade-offs among different objectives [27,28,44], in reality, compromise solutions need to involve key stakeholders [78] and equity assessments across communities and sectors [79,80]. Advances in multiobjective optimization, more interactive software facilitating stakeholder engagement, and more case study examples are needed to improve the way we explicitly balance trade-offs in SCP.

Including social and cultural dimensions

While SCP typically integrates ecological principles, it often includes limited social and cultural dimensions or focuses on a narrow set of values for nature [81]. Indigenous and other communities may perceive conservation and associated costs differently [82]. Their values may prioritize nonmonetary aspects, such as knowledge, spirituality, language, territory, or other cultural aspects, over biodiversity or economic benefits. Incorporating social and cultural dimensions in SCP would value **conservation areas** by better including nature's contributions to people and incorporating social equity. This would include Indigenous peoples' and local community rights, knowledge, and values to improve legitimacy and ownership while addressing cobenefits and trade-offs in planning decisions. This diversity of perspectives highlights the need to broaden our understanding and approach to SCP using a more inclusive lens [83,84].

Bridging the gap between science and practice

The adoption of SCP by practitioners faces substantial challenges, rooted in both sectoral interests and systemic issues, such as the lack of coordination among different legislation and policy frameworks (e.g., environmental versus agricultural management). Different sectors and levels of government, often working in silos, set policy targets for a range of user groups, often competing for the same space or resources. Such uncoordinated approaches hinder synergies among sectors and impede the implementation of SCP, leading to fragmented, incoherent, and ineffective conservation strategies [34]. Tighter integration of SCP into intersectoral spatial planning schemes and frameworks, such as Strategic Environmental Assessments, Biodiversity Offsetting, and Marine Spatial Planning (Box 3), could facilitate cross-sectoral collaboration; equal footing among sectors; and estimation of trade-offs and synergies among ecological, social, and economic planning objectives (e.g., [85]).

SCP implementation demands robust data, encompassing ecological features and human uses. Detailed and up-to-date data are often lacking or incomplete, leading to SCP applications that are only partially representative of the particular management problem, eliciting criticism by

stakeholders [86]. Moreover, decision-makers sometimes find it difficult to effectively apply the complex models and trade-offs associated with various SCP key elements, including spatiotemporal connectivity, climate change, and cumulative impacts on ecosystems. Building trust in the scientific process and communicating the reliability of SCP approaches to decision-makers is essential [87]. Standardizing communication of key modeling decisions and gaps potentially influencing trade-offs in conservation plans could improve acceptance of SCP by decision-makers. Making SCP tools accessible, providing license-free options for user-friendly tools, and effectively communicating these complex processes to legislators and decision-makers are imperative. This necessitates diversifying working groups by including science brokers adept at translating research findings for nonexpert audiences [88].

To ensure that knowledge and experience persist and grow within institutions and among practitioners in government and environmental non-governmental organizations (NGOs), communities of practice could play a key role. Practical guidance, including the development of comprehensive manuals and toolkits, can facilitate this process [89]. Accessible targeted training courses for administrators, politicians, and industry leaders can bridge the gap between science and practice in SCP. These necessitate a strategic reframing of terminology and an understanding of how political processes can impede practical SCP implementation. In parallel, promoting SCP as a profession (with certification) that follows standardized training through a recognized curriculum could ensure better uptake of SCP on the ground.

Concluding remarks

SCP offers a robust framework for achieving objectives outlined in the GBF. Recent advances in optimization tools have broadened their functionality and scope and enhanced their effectiveness in meeting SCP objectives. Some advances focus on the more technical aspects of spatial

Outstanding questions

How can we account for the dynamics of multiple species' movements and set ecologically meaningful targets for representation and changes in connectivity patterns in the objective function of optimization tools?

How can we effectively incorporate the iterative process of monitoring, evaluation, and learning into spatial prioritization? Decisions are made in changing contexts and depend on future conditions that may vary over time, and thus dynamic prioritization and decision-making require information on what conditions are more likely over different time periods.

How can AI increase the capacity of optimization tools to better address SCP principles?

How can we better estimate and report uncertainty in conservation plans and especially in climate-smart planning, considering climate-induced changes of conservation features and human activities?

How can SCP scientists better engage stakeholders and optimization tools better estimate and present trade-offs among ecological, social, and economic objectives for cross-sectoral collaboration and increase biodiversity outcomes in intersectoral planning?

How can SCP address diverse knowledge systems associated with indigenous and local communities, including spiritual values not amenable to spatial visualization and/or quantitative analysis?

How can optimization tools be enhanced, data challenges improved, and institutional barriers overcome to integrate multirealm and multidimensional considerations across time and space?

Box 3. Integrating SCP into marine spatial planning

Marine spatial planning (MSP) is an integrative public process that strives to balance environmental protection with the sustainable use of the sea and address conflicts for the use of marine space [104]. Worldwide, legal frameworks mandate the development of marine spatial plans to delineate sea usage. For example, the EU MSP Directive requires all coastal member states to develop and periodically update such plans.

The MSP framework (Figure I) is a broad process encompassing a wide range of methods, tools, and approaches. However, the nonspecificity of robust scientific tools within the MSP process can result in confusion, delays, suboptimal planning, and potentially adverse outcomes for biodiversity conservation. This emphasizes the importance of integrating SCP into MSP [87,105]. SCP facilitates the identification of areas or management measures that effectively safeguard marine biodiversity and ecosystem functions while balancing multiple objectives, including socioeconomic interests. The flexibility and adaptability of SCP allows it to accommodate distinct sectoral interests, ecological conditions, and sociocultural settings (MSP Step 5, Figure I outer blue circle). To meet the Global Biodiversity Framework targets, nations can harness the SCP framework to tailor strategies that effectively balance conservation with economic sustainability within their MSP processes. Such an example is South Africa, where marine protection increased tenfold after a 15-year process, aligning MSP objectives and spatial priorities across sectors with similar requirements for ecosystem health and environmental management [56,87].

A central aspect of MSP is the negotiation process among stakeholders, including industries, conservationists, and policy-makers (MSP Step 4, Figure I, outer blue circle). This interaction is pivotal for optimizing SCP by aligning collective values and preferences, assessing synergies and trade-offs, ensuring transparency, and the successful implementation of SCP strategies (MSP Steps 7 and 8, Figure I, outer blue circle). Thus, integrating SCP into MSP necessitates a comprehensive evaluation of different knowledge systems and perceptions related to marine uses and conservation.

Scenario analysis is a crucial step in a balanced MSP process, and it can benefit substantially from SCP contribution in delivering conservation targets (MSP Steps 3 and 6, Figure I, outer blue circle). This aids informed scrutiny of policy options, underpinned by quantified data and visually supported by mapped alternatives. Leveraging opportunities for spatial planning within emerging sectors, such as renewable energy and nature repair markets, can provide initial motivation and common ground for different interests, facilitating SCP integration.

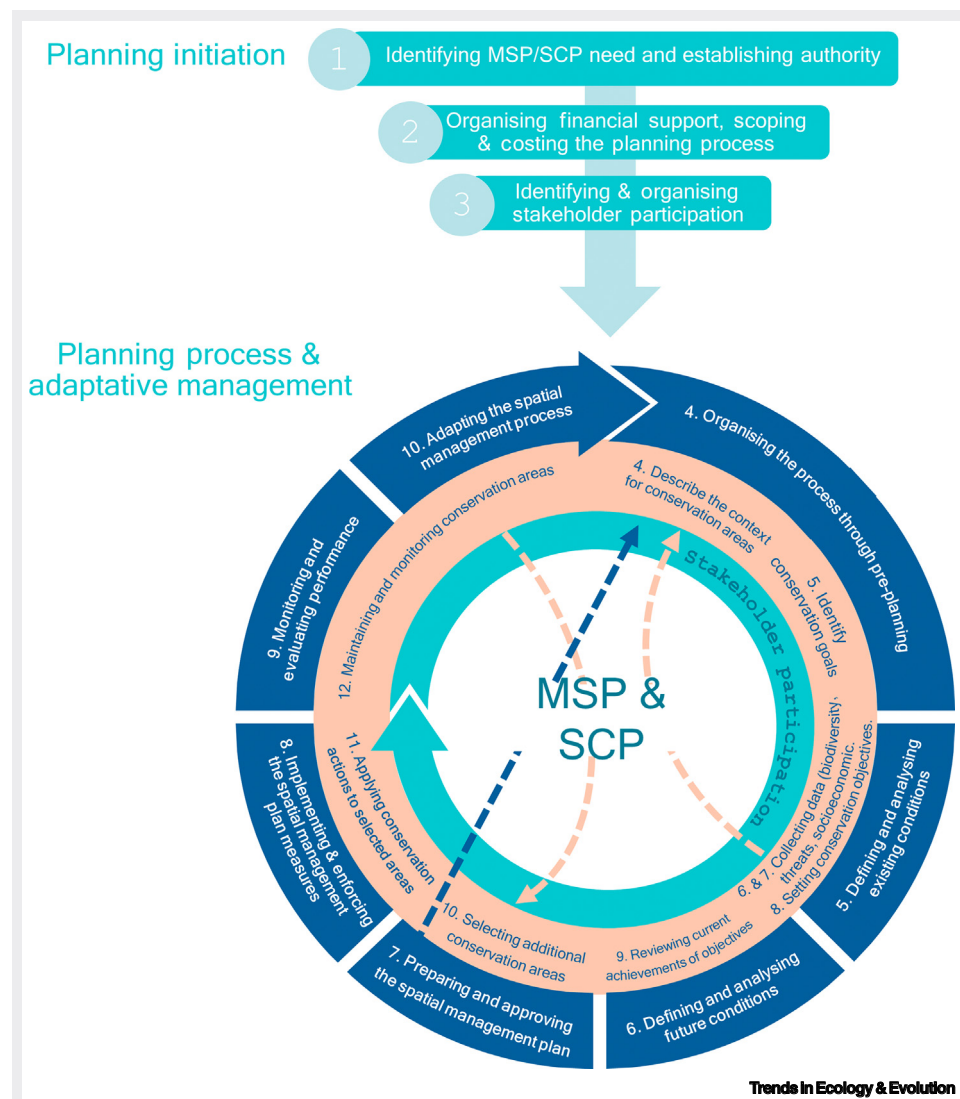


Figure 1. The diagram illustrates the process and alignment of the UNESCO marine spatial planning approach [104] with the framework of systematic conservation planning (SCP) [3]. Embedding and simultaneously addressing SCP key steps (shown in the inner orange circle) alongside marine spatial planning (MSP) (steps shown in outer blue circle) would support 'best practices' for ensuring that biodiversity values, environmental threats, and management actions are adequately captured within a spatial plan. Stakeholder partnerships and involvement are recommended throughout the process. Abbreviation: UNESCO, United Nations Educational, Scientific and Cultural Organization.

prioritization (e.g., the use of exact algorithms and AI improving planning solutions' quality); others are concerned with conceptual SCP aspects (e.g., broadening the spectrum of objectives and biodiversity representativeness), and still others focus on outreach and stakeholder engagement. Future SCP research should aim to address pressing theoretical, technical, and implementation challenges (see [Outstanding questions](#)). These questions could be answered by developing methods for better integrating spatiotemporal connections and changes into planning, quantifying and communicating uncertainty, dealing with trade-offs when planning for multiple objectives, and including social and cultural dimensions in SCP. Addressing these issues will enhance the available

tools and methods so that they provide greater flexibility in problem formulation and better solve complex problems. Mainstreaming SCP concepts, tools, and methods into policy is key for improving the allocation of limited resources for biodiversity conservation.

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Declaration of interests

The authors have no interests to declare.

References

- Convention on Biological Diversity (2022) Final text of Kunming-Montreal Global Biodiversity Framework. <https://www.cbd.int/article/cop15-final-text-kunming-montreal-gbf-221222>
- Margules, R.C. and Pressey, L.R. (2000) Systematic conservation planning. *Nature* 405, 243–253
- Pressey, L.R. and Bottrill, C.M. (2009) Approaches to landscape and seascape-scale conservation planning: convergence, contrasts and challenges. *Oryx* 43, 464–475
- Sinclair, P.S. *et al.* (2018) The use, and usefulness, of spatial conservation prioritizations. *Conserv. Lett.* 11, e12459
- Adams, M.V. *et al.* (2019) Implementation strategies for systematic conservation planning. *Ambio* 48, 139–152
- Tallis, H. *et al.* (2021) Prioritizing actions: spatial action maps for conservation. *Ann. N. Y. Acad. Sci.* 1505, 118–141
- Ball, R.I. *et al.* (2009) Marxan and relatives: software for spatial conservation prioritization. In *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools* (Mollanen, A. *et al.*, eds), pp. 185–195, Oxford University Press
- Mollanen, A. *et al.* (2009) A mathematical classification of conservation prioritization problems. In *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools* (Mollanen, A. *et al.*, eds), pp. 28–42, Oxford University Press
- Mollanen, A. *et al.* (2022) Novel methods for spatial prioritization with applications in conservation, land use planning and ecological impact avoidance. *Methods Ecol. Evol.* 13, 1062–1072
- Kukkala, S.A. and Mollanen, A. (2013) Core concepts of spatial prioritisation in systematic conservation planning. *Biol. Rev.* 88, 443–464
- Beyer, H.L. *et al.* (2016) Solving conservation planning problems with integer linear programming. *Ecol. Model.* 328, 14–22
- Daigle, R.M. *et al.* (2020) Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect. *Methods Ecol. Evol.* 11, 570–579
- Schuster, R. *et al.* (2020) Exact integer linear programming solvers outperform simulated annealing for solving conservation planning problems. *PeerJ* 8, e9258
- Van Mantgem, S.E. *et al.* (2023) Coco: conservation design for optimal ecological connectivity. *Front. Ecol. Evol.* 111149571. <https://doi.org/10.3389/fevo.2023.1149571>
- Silvestro, D. *et al.* (2022) Improving biodiversity protection through artificial intelligence. *Nat. Sustain.* 5, 415–424
- Carvalho, B.S. *et al.* (2017) Spatial conservation prioritization of biodiversity spanning the evolutionary continuum. *Nat. Ecol. Evol.* 1, 0151
- Andreollo, M. *et al.* (2022) Evolving spatial conservation prioritization with intraspecific genetic data. *Trends Ecol. Evol.* 37, 553–564
- Nielsen, S.E. *et al.* (2023) Molecular ecology meets systematic conservation planning. *Trends Ecol. Evol.* 38, 143–155
- Pollock, J.L. *et al.* (2017) Large conservation gains possible for global biodiversity facets. *Nature* 546, 141–144
- Brumm, J.K. *et al.* (2021) Accounting for multiple dimensions of biodiversity to assess surrogate performance in a freshwater conservation prioritization. *Ecol. Indic.* 122, 107320
- Pollock, J.L. *et al.* (2020) Protecting biodiversity (in all its complexity): new models and methods. *Trends Ecol. Evol.* 35, 1119–1128
- Muenzel, D. *et al.* (2024) Combining environmental DNA and visual surveys can inform conservation planning for coral reefs. *Proc. Natl. Acad. Sci. U. S. A.* 121, e2307214121
- Villarreal-Rosas, J. *et al.* (2020) Advancing systematic conservation planning for ecosystem services. *Trends Ecol. Evol.* 35, 1129–1139
- Neugarten, R.A. *et al.* (2024) Mapping the planet's critical areas for biodiversity and nature's contributions to people. *Nat. Commun.* 15, 261
- Perschke, M.J. *et al.* (2024) Systematic conservation planning for people and nature: biodiversity, ecosystem services, and equitable benefit sharing. *Ecosyst. Serv.* 68, 101637
- Staden, V.L. *et al.* (2022) An evaluation of the effectiveness of critical biodiversity areas, identified through a systematic conservation planning process, to reduce biodiversity loss outside protected areas in South Africa. *Land Use Policy* 115, 106044
- Virtanen, E.A. *et al.* (2022) Balancing profitability of energy production, societal impacts and biodiversity in offshore wind farm design. *Renew. Sust. Energ. Rev.* 158, 112087
- Law, E.A. *et al.* (2017) Mixed policies give more options in multifunctional tropical forest landscapes. *J. Appl. Ecol.* 54, 51–60
- Salgado-Rojas, J. *et al.* (2023) prioriactions: Multi-action management planning in R. *Methods Ecol. Evol.*, Published online October 4, 2023. <https://doi.org/10.1111/2041-210X.14220>
- Barbosa, A. *et al.* (2019) Cost-effective restoration and conservation planning in green and blue infrastructure designs. A case study on the Intercontinental Biosphere Reserve of the Mediterranean: Andalusia (Spain) – Morocco. *Sci. Total Environ.* 652, 1463–1473
- Justeau-Alaire, D. *et al.* (2023) restopr: an R package for ecological restoration planning. *Restor. Ecol.* 31, e13910
- Beger, M. *et al.* (2022) Demystifying ecological connectivity for actionable spatial conservation planning. *Trends Ecol. Evol.* 37, 1079–1091. <https://doi.org/10.1016/j.tree.2022.09.002>
- Muenzel, D. *et al.* (2023) Comparing spatial conservation prioritization methods with site- versus spatial dependency-based connectivity. *Conserv. Biol.* 37, e14008
- Álvarez-Romero, J.G. *et al.* (2011) Integrated land-sea conservation planning: the missing links. *Annu. Rev. Ecol. Syst.* 42, 381–409
- Giakoumi, S. *et al.* (2019) Conserving European biodiversity across realms. *Conserv. Lett.* 12, e12586
- Hermoso, V. *et al.* (2022) Conservation planning across realms: enhancing connectivity for multi-realm species. *J. Appl. Ecol.* 58, 644–654
- Tulloch, V.J.D. *et al.* (2021) Minimizing cross-realm threats from land-use change: a national-scale conservation framework connecting land, freshwater and marine systems. *Biol. Conserv.* 254, 108954
- West, D.W. *et al.* (2019) Approaches to the selection of a network of freshwater ecosystems within New Zealand for conservation. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 29, 1574–1586

39. Carroll, C. *et al.* (2017) Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. *Glob. Chang. Biol.* 23, 4508–4520
40. Brito-Morales, I. *et al.* (2018) Climate velocity can inform conservation in a warming world. *Trends Ecol. Evol.* 33, 441–457
41. Frazão Santos, C. *et al.* (2020) Integrating climate change in ocean planning. *Nat. Sustain.* 3, 505–516
42. Lawler, J.J. *et al.* (2020) Planning for climate change through additions to a national protected area network: implications for cost and configuration. *Philos. Trans. R. Soc. B Biol. Sci.* 375, 20190117
43. Arafeh-Dalmau, N. *et al.* (2021) Incorporating climate velocity into the design of climate-smart networks of marine protected areas. *Methods Ecol. Evol.* 12, 1969–1983
44. Fourchault, L. *et al.* (2024) Generating affordable protection of high seas biodiversity through cross-sectoral spatial planning. *One Earth* 7, 253–264
45. Álvarez-Romero, J.G. *et al.* (2018) Designing connected marine reserves in the face of global warming. *Glob. Chang. Biol.* 24, e671–e691
46. Arafeh-Dalmau, N. *et al.* (2023) Integrating climate adaptation and transboundary management: guidelines for designing climate-smart marine protected areas. *One Earth* 6, 1523–1541
47. Schmaljohann, H. and Both, C. (2017) The limits of modifying migration speed to adjust to climate change. *Nat. Clim. Chang.* 7, 573–576
48. Gerber, R.L. *et al.* (2014) Climate change impacts on connectivity in the ocean: implications for conservation. *Ecosphere* 5, 1–18
49. Zhang, W. *et al.* (2023) Prioritizing global conservation of migratory birds over their migration network. *One Earth* 6, 1340–1349
50. Venegas-Li, R. *et al.* (2018) 3D spatial conservation prioritisation: accounting for depth in marine environments. *Methods Ecol. Evol.* 9, 773–784
51. Brito-Morales, I. *et al.* (2022) Towards climate-smart, three-dimensional protected areas for biodiversity conservation in the high seas. *Nat. Clim. Chang.* 12, 402–407
52. Doxa, A. *et al.* (2022) 4D marine conservation networks: Combining 3D prioritization of present and future biodiversity with climatic refugia. *Glob. Chang. Biol.* 28, 4577–4588
53. Linke, A. *et al.* (2019) 3D conservation planning: Including aquifer protection in freshwater plans refines priorities without much additional effort. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 29, 1063–1072
54. Jorda, G. *et al.* (2019) Ocean warming compresses the three-dimensional habitat of marine life. *Nat. Ecol. Evol.* 4, 109–114
55. Chauvier-Mendes, Y. *et al.* (2024) Transnational conservation to anticipate future plant shifts in Europe. *Nat. Ecol. Evol.* 8, 454–466
56. Sink, J.K. *et al.* (2023) Integrated systematic planning and adaptive stakeholder process support a 10-fold increase in South Africa's Marine Protected Area estate. *Conserv. Lett.* 16, e12954
57. Dunn, D.C. *et al.* (2016) Dynamic ocean management increases the efficiency and efficacy of fisheries management. *Proc. Natl. Acad. Sci.* 113, 668–673
58. Runge, C.A. *et al.* (2016) Incorporating dynamic distributions into spatial prioritization. *Divers. Distrib.* 22, 332–343
59. Grantham, H.S. *et al.* (2013) A comparison of zoning analyses to inform the planning of a marine protected area network in Raja Ampat, Indonesia. *Mar. Policy* 38, 184–194
60. Makino, A. *et al.* (2014) Spatio-temporal marine conservation planning to support high-latitude coral range expansion under climate change. *Divers. Distrib.* 20, 859–871
61. Vermeulen-Miltz, E. *et al.* (2023) A system dynamics model to support marine spatial planning in Algoa Bay, South Africa. *Environ. Model. Softw.* 160, 105601
62. Possingham, H.P. *et al.* (2009) Accounting for habitat dynamics in conservation planning. In *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools* (Moilanen, A. *et al.*, eds), pp. 135–144, Oxford University Press
63. Wen, X. *et al.* (2024) Review of terrestrial temporarily conserved areas in Canada, the United States, and Mexico. *Conserv. Biol.* 38, e14160
64. Vigo, M. *et al.* (2024) Dynamic marine spatial planning for conservation and fisheries benefits. *Fish Fish.* 25, 630–646
65. Margis, R.A. *et al.* (2017) Integrated conservation planning for coral reefs: designing conservation zones for multiple conservation objectives in spatial prioritisation. *Glob. Ecol. Biogeogr.* 11, 53–68
66. Tittensor, D.P. *et al.* (2023) Integrating climate adaptation and biodiversity conservation in the global ocean. *Sci. Adv.* 5, eaay9969
67. Kujala, H. *et al.* (2013) Treatment of uncertainty in conservation under climate change. *Conserv. Lett.* 6, 73–85. <https://doi.org/10.1111/j.1755-263X.2012.00299.x>
68. Langford, T.W. *et al.* (2011) Raising the bar for systematic conservation planning. *Trends Ecol. Evol.* 26, 634–640
69. Kujala, H. *et al.* (2018) Spatial characteristics of species distributions as drivers in conservation prioritization. *Methods Ecol. Evol.* 9, 1121–1132
70. Guillera-Aroita (2015) Is my species distribution model fit for purpose matching data. *Glob. Ecol. Biogeogr.* 24, 276–292
71. Armsworth, R.P. (2014) Inclusion of costs in conservation planning depends on limited datasets and hopeful assumptions. *Ann. N. Y. Acad. Sci.* 1322, 61–76
72. Mazar, T. *et al.* (2014) Large-scale conservation planning in a multinational marine environment: cost matters. *Ecol. Appl.* 24, 1115–1130. <https://doi.org/10.1890/13-1249.1>
73. García-Barón, I. *et al.* (2020) The value of time-series data for conservation planning. *J. Appl. Ecol.* 58, 608–619
74. Cork, S. *et al.* (2023) Exploring alternative futures in the Anthropocene. *Annu. Rev. Environ. Resour.* 48, 25–54
75. Popov, V. *et al.* (2022) Managing risk and uncertainty in systematic conservation planning with insufficient information. *Methods Ecol. Evol.* 13, 230–242
76. Jung, M. *et al.* (2021) Areas of global importance for conserving terrestrial biodiversity, carbon and water. *Nat. Ecol. Evol.* 5, 1499–1509
77. Sala, E. *et al.* (2021) Protecting the global ocean for biodiversity, food and climate. *Nature* 592, 397–402
78. Law, E.A. *et al.* (2018) Equity trade-offs in conservation decision making. *Conserv. Biol.* 32, 294–303
79. Halpern, B.S. *et al.* (2013) Achieving the triple bottom line in the face of inherent trade-offs among social equity, economic return, and conservation. *Proc. Natl. Acad. Sci.* 110, 6229–6234
80. Gissi, E. *et al.* (2018) Addressing transboundary conservation challenges through marine spatial prioritization. *Conserv. Biol.* 32, 1107–1117
81. Pascual, U. *et al.* (2023) Diverse values of nature for sustainability. *Nature* 620, 813–823
82. Thondhlana, G. *et al.* (2020) Non-material costs of wildlife conservation to local people and their implications for conservation interventions. *Biol. Conserv.* 246, 108578
83. Ban, N.C. *et al.* (2013) A social-ecological approach to conservation planning: embedding social considerations. *Front. Ecol. Environ.* 11, 194–202
84. Iwamura, T. *et al.* (2018) Considering people in systematic conservation planning: insights from land system science. *Front. Ecol. Environ.* 16, 388–396
85. Boussarie, G. *et al.* (2023) Marine spatial planning to solve increasing conflicts at sea: a framework for prioritizing offshore windfarms and marine protected areas. *J. Environ. Manag.* 339, 117857
86. Janßen, H. *et al.* (2019) Knowledge integration in marine spatial planning: a practitioners' view on decision support tools with special focus on Marxan. *Ocean Coast. Manag.* 168, 130–138
87. Holness, S.D. *et al.* (2022) Using systematic conservation planning to align priority areas for biodiversity and nature-based activities in marine spatial planning: a real-world application in contested marine space. *Biol. Conserv.* 271, 109574
88. Gluckman, P.D. *et al.* (2021) Brokerage at the science-policy interface: from conceptual framework to practical guidance. *Humanit. Soc. Sci. Commun.* 8, 1–10
89. Jung, M. *et al.* (2024) An assessment of the state of conservation planning in Europe. *Philos. Trans. R. Soc. B* 379, 20230015
90. Watts, M. *et al.* (2021) Software for prioritizing conservation actions based on probabilistic information. *Conserv. Biol.* 35, 1299–1308

91. Watts, M.E. *et al.* (2009) Marxan with zones: software for optimal conservation based land- and sea-use zoning. *Environ. Model. Softw.* 24, 1513–1521
92. Hanson, J.O. *et al.* (2024) Systematic conservation prioritization with the prioritizr R package. *Conserv. Biol.*, e14376
93. Hermoso, V. *et al.* (2012) Using water residency time to enhance spatio-temporal connectivity for conservation planning in seasonally dynamic freshwater ecosystems. *J. Appl. Ecol.* 49, 1028–1035
94. Watson, J.E.M. *et al.* (2011) Systematic conservation planning: past, present and future. In *Conservation Biogeography* (1st Ed.) (Ladle, R.J. and Whittaker, R.J., eds), pp. 136–160, Wiley
95. Kirkpatrick, S. *et al.* (1983) Optimization by simulation by annealing. *Science* 220, 671–680
96. Gelfand, A.E. and Shirota, S. (2019) Preferential sampling for presence/absence data and for fusion of presence/absence data with presence-only data. *Ecol. Monogr.* 89, e01372
97. Cosentino, F. and Maiorano, L. (2021) Is geographic sampling bias representative of environmental space? *Ecol. Inform.* 64, 101369
98. Renner, I.W. *et al.* (2015) Point process models for presence-only analysis. *Methods Ecol. Evol.* 6, 366–379
99. Bachl, E.F. *et al.* (2019) inlabru: an R package for Bayesian spatial modelling from ecological survey data. *Methods Ecol. Evol.* 10, 760–766
100. Martino, S. *et al.* (2021) Integration of presence-only data from several sources: a case study on dolphins' spatial distribution. *Ecography* 44, 1533–1543
101. Moilanen, A. *et al.* (2006) Uncertainty analysis for regional-scale reserve selection. *Conserv. Biol.* 20, 1688–1697
102. Muscatello, A. *et al.* (2021) How decisions about fitting species distribution models affect conservation outcomes. *Conserv. Biol.* 35, 1309–1320
103. Panunzi, G. *et al.* (2024) Estimating the spatial distribution of the white shark in the Mediterranean Sea via an integrated species distribution model accounting for physical barriers. *Environmetrics* e2876,
104. Ehler, C. and Douvère, F. (2009) *Marine spatial planning: a step-by-step approach toward ecosystem-based management*. Intergovernmental Oceanographic Commission and Man and the Biosphere Programme. IOC Manual and Guides No. 53
105. Markantonatou, V. *et al.* (2021) Marine spatial plans focusing on biodiversity conservation: the case of the Aegean Sea. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 31, 2278–2292