

Conservation planning in a changing world

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Conservation planning is the process of locating, configuring, implementing and maintaining areas that are managed to promote the persistence of biodiversity and other natural values. Conservation planning is inherently spatial. The science behind it has solved important spatial problems and increasingly influenced practice. To be effective, however, conservation planning must deal better with two types of change. First, biodiversity is not static in time or space but generated and maintained by natural processes. Second, humans are altering the planet in diverse ways at ever faster rates.

Systematic conservation planning

Systematic conservation planning [1] identifies configurations of complementary areas that achieve explicit, and generally quantitative, objectives. Since its origin in the early 1980s, the field has influenced planning by major organizations such as The Nature Conservancy [2], shaped policy, legislation and conservation on the ground [3], and featured in almost 200 presentations at meetings of the Society for Conservation Biology. The hundreds of publications in the field reflect not only advances in ideas, techniques and relevance, but also its short history and main limitations. Most publications concern biodiversity pattern (Figure 1) – that is, the elements of biodiversity that can be mapped and regarded as static [4]. Planners have done less well at promoting the persistence of the myriad ecological and evolutionary processes that maintain and generate biodiversity [5]. Most systematic methods have also assumed implicitly that threats to biodiversity are absent or static [6] (Figure 1). Planners might recognize previous losses of biodiversity, even the legacies of continuing loss from past threats, but might not anticipate the rates and patterns of dynamic threats [5,7]. Work on these limitations is underway. The increasing influence of systematic methods on conservation spending and actions underlines the importance and urgency of further advances. Our aim here is to summarize ideas, techniques and unresolved issues in two main areas: planning for biodiversity processes, and planning in the context of dynamic threats. We then consider the intersection of these two problems (Figure 1d), which has received least

attention but presents the most compelling challenges. Systematic conservation planning has enormous potential to rise to these challenges, partly through science and partly through closer connections between scientists and practitioners [3].

Planning for biodiversity processes

Biodiversity processes are sequences of changes in biological and physical characteristics, from molecular to global in scale. They include the birth, death and movement of individual organisms, local extinctions and recolonizations of populations, herbivory, predation, patch dynamics, seasonal migrations, adjustment of the distributions of species to changing climate, and speciation [8–11]. There are two reasons for considering processes in conservation planning. First, most of our depictions of biodiversity are snapshots [5], which become outdated as species distributions change and categories of land, sea and freshwater blur and shift. Second, biodiversity is generated and maintained by processes and, unless we plan for them specifically, many processes will be disrupted or cease altogether. The reasons include direct removal by deforestation, damming of rivers, overharvesting of top marine predators, invasive species and reduction of connectivity and population sizes through fragmentation. The consequences are loss of species and reduced evolutionary potential of many that remain [5,12–16]. Mitigating these effects does not require pattern to be abandoned because at least pattern tells us where biodiversity is now. It requires planning for both pattern and process (Figure 1b).

Ideally, ‘the purpose of a nature reserve is to maintain, hopefully for perpetuity, a highly complex set of ecological, genetic, behavioural, evolutionary and physical processes and the coevolved, compatible populations which participate in those processes’ [17]. Faced with this complexity, and the fact that conservation areas will occupy only parts of most regions, planners must address three questions: (i) which processes to plan for?; (ii) how to plan for processes?; and (iii) how to choose between processes when conservation resources are insufficient for all to persist?

Which processes to plan for?

In any region, the list of biological and physical processes is endless [17], so planners apply a series of filters. The first selects processes that they know about. Of those, the

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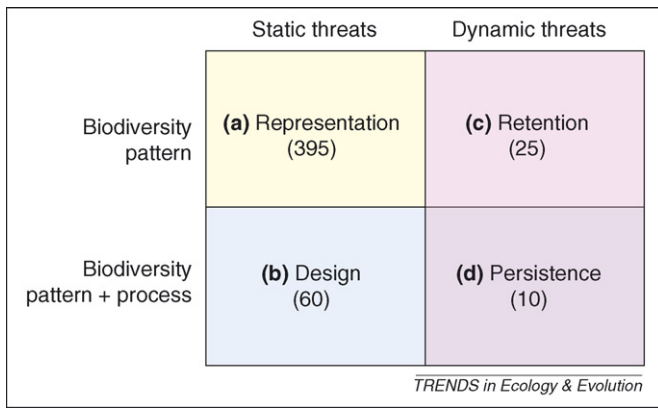


Figure 1. Four ways of doing systematic conservation planning. (a–d) are defined by the biodiversity features considered (rows) and assumptions about threats to biodiversity (columns), adapted from Ref. [43]. Figures in parentheses are estimated numbers of journal papers and book chapters on systematic conservation planning that apply to each quadrant (from R.L.P.’s literature database). Minimum criteria for inclusion of publications were: (i) use of explicit targets for biodiversity features; and (ii) methods involving complementarity to recommend areas for conservation action. The bulk of the literature covers representation of biodiversity pattern assuming static threats (a). This provides part of the foundation for extending methods into other quadrants. (b–d) correspond to sections of this review. Design (b) is shorthand for methods that address biodiversity processes but not dynamic threats. Retention [6] (c) acknowledges dynamic threats but deals only with biodiversity pattern. Maximizing the persistence of biodiversity (d) requires attention to both biodiversity processes and dynamic threats.

second filter selects processes that are understood well enough for their spatial requirements to be interpreted. Of those, the third filter selects processes for which conservation planning can make a difference. Physical and biological processes operate across a wide range of spatial and temporal scales. Fine-scale processes, such as many pollinator–plant interactions, will be accommodated in most conservation areas without specific planning [8,9]. Extensive processes, such as climate, ocean currents and plate tectonics, are beyond the influence of conservation planning, although the effects of climate change might be anticipated and influence conservation decisions [18,19]. Between these scales, the persistence of processes will be determined, at least partially, by conservation planning [9]. These dependent processes include ‘natural’ [20] patch dynamics, the persistence of metapopulations, dispersal of marine larvae, altitudinal migration and continuing evolution of species.

How to plan for processes?

Planning only for biodiversity pattern is likely to jeopardize the persistence of many processes, especially those requiring conservation management over large or specially configured areas [9]. We describe four compatible approaches to planning for processes: (i) variable representation targets; (ii) moveable conservation areas; (iii) spatial catalysts; and (iv) design criteria. Representation targets define the amount of each biodiversity feature that should be contained within a system of conservation areas [9]. Although uniform percentages have often been used, variable targets recognize that features differ in their conservation requirements. Examples of variable targets relating to biodiversity processes include estimates of viable population sizes and their corresponding areas, adjusted to account for life-history characteristics and

responses to disturbance [21], and insurance multipliers for targets that account for proportions of conservation systems that are likely to be affected by natural [20] disturbances at any time [22]. Targets could also recognize the relative phylogenetic diversity associated with species [10].

Some moveable conservation areas are applied and removed as features of interest shift between parts of a planning region. They have been proposed to enable regeneration of trees in grazed landscapes [23] and to track species that occur patchily in space and time [24,25]. Other moveable conservation areas are temporary but spatially fixed restrictions on extractive uses, intended to protect species when they are particularly vulnerable or to enable populations to recover from harvesting. In arid Australia, native species such as small mammals contract into refugia during drought, where their persistence, and later expansion into less favourable areas, could be promoted by periodic exclusion of grazing stock [26]. Short-term fishing closures have been applied extensively for various purposes that include protecting spawning aggregations [27] and maintaining yields of desirable species. In general, moveable conservation areas are probably easier to apply in marine environments without the static property rights on land and when they enable some extractive use, limit recreational use rather than livelihoods, and are small.

Planners can also identify surrogates for processes [28] in the form of spatial catalysts*. These features are spatially fixed for the purposes of most planning horizons but important for the continuation of processes of interest. Several examples come from the Cape Floristic Region of South Africa [29], including sinuous, narrow interfaces between alkaline and acid soils related to diversification of some plant lineages (Box 1). Spatial catalysts are defined by structural attributes of regions, such as topography, geology, soils and vegetation, sometimes combined with variables such as climate or ocean currents. Some are identified by their associated biological phenomena. They differ widely in extent and configuration, and sustain various ecological and evolutionary dynamics. Examples outside the Cape region are ecotones between rainforest and savanna as drivers of diversification [30], putative refugia where species might ride out climatic fluctuations [31], seamounts and marine upwellings [25] and migratory staging areas. The list of spatial catalysts for any region will probably be idiosyncratic, depending on available information and its environment, biota and biogeographical history. Spatial catalysts have two roles in conservation planning. As features to be managed for conservation, they have their own requirements for continued functioning and influence the configuration of regional conservation systems [28,29] while also contributing to targets for other coincident features. Spatial catalysts can also demarcate historical influences on species composition through, for example, isolation by large rivers [32], mountain building

* Previous terms for spatial catalysts are ‘fixed spatial components’ or ‘fixed surrogates’, which acknowledge their static nature and contrast them with aspects of design, such as alignment, shape and replication, that leave planners with spatial flexibility in deciding on the configuration of conservation areas [28]. We use the new term ‘spatial catalysts’ to emphasize the distinction between these static but process-related features and the more widely used surrogates for biodiversity pattern.

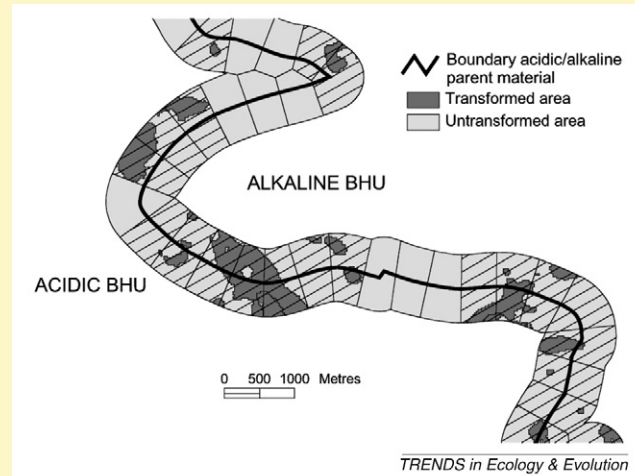
Box 1. Examples of spatial catalysts

Conservation planning for the Cape Floristic Region of South Africa (Figure I) identified four categories of spatial catalyst [28]: edaphic interfaces (edges between contrasting soil types); upland–lowland interfaces; movement corridors of marine sands; and major riverine corridors that crossed chains of mountains. All seem to be important in sustaining ecological and evolutionary processes. The edaphic interface in Figure II and others of its type mark the boundaries between soils with strongly contrasting chemical compositions, shown here as different broad habitat units (BHUs). They are believed to be associated with past and probably future diversification of some plant lineages [9,29]. Some edaphic interfaces are also associated with strong differences in landform (Figure III).



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Figure I. View of a global biodiversity hotspot. In the Cape Floristic Region, lowland habitats such as the renosterveld shrubland in the foreground have been extensively transformed for agriculture. This has drastically narrowed the spatial options for representing biodiversity pattern in conservation areas [28] and reduced the potential to plan for processes. Movements of animals between these lowlands and the fynbos-clad mountains in the distance, for example, have been curtailed. Native vegetation associated with spatial catalysts such as upland–lowland interfaces and edaphic interfaces [29] has also been extensively removed. Photo: R.M. Cowling.



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Figure II. An edaphic interface mapped for conservation planning. This is one of eight types of edaphic interface identified and targeted in the Cape Floristic Region of South Africa [9,28]. The eight types were defined by unique combinations of alkaline and acidic soil types mapped as different BHUs. Sections of the interfaces that were used as planning units (units of comparison and selection for conservation management) were defined at 500 m intervals along their lengths and each section extended an arbitrary distance of 500 m on either side. Transformed areas were covered by agriculture or high-density alien plants, but hatching indicates that these areas are potentially restorable, unlike areas elsewhere that were covered by urban development. Reproduced with permission from [29] and modified with permission from the senior author.



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Figure III. An edaphic interface on the ground. In this part of the Cape Floristic Region, relatively nutrient-rich, clayey soils derived from shale bedrock (foreground) interface abruptly with nutrient-poor, sandy soils associated with quartzitic sandstones that form the Cape Fold Mountains. Across this interface are remarkably large changes in species composition and strong selection on individual plants that establish off their parent soils. Photo: J. Vlok.

[33] or climatic variation. As such, they might not need specific conservation management. Their role is then to improve the subdivision of planning regions into more biologically homogeneous parts by complementing environmental information (pattern) with information on biogeographical history (process) [10,34].

By ‘design criteria’, we mean aspects of configuration of conservation areas or entire conservation systems. Criteria include size, shape, connectivity (defined variously) [35], replication, spacing and directional alignment. Among the motivations for these criteria are increasing the persistence of fragmented populations, buffering streams from

pollution, accommodating patch dynamics, promoting adjustment of ranges to climate change, insuring against catastrophes and facilitating management [8,17,28,35–37]. Design criteria have been defined specifically or generically, with or without quantitative objectives related to the requirements of particular processes, respectively. Generic definitions[†] have been part of conservation planning for decades. They are still commonly used, mainly

[†] Generic criteria for connectivity have been described as ‘structural’ [35]. These are derived from physical characteristics of the landscape, such as size, shape and location of habitat patches but without information on the potential dispersal ability of organisms or observations of actual dispersal between patches.

Box 2. Planning for biodiversity processes with a generic design criterion

Generic design criteria can be applied by using conservation planning software interactively [38] or to automate selections of areas to produce the desired configuration [37]. Two examples here illustrate automated selections using the MARXAN software applied to north-eastern New South Wales. Areas are grid squares covering 4 hectares (200 m × 200 m). Pattern features are 107 forest types, each with a conservation target in hectares, described by Pressey *et al.* [6]. Figure 1a shows irreplaceability values, indicating the likelihood of each area being included in an expanded conservation system that minimizes the total extent of land required to achieve a dual objective: targets for all forest types and a degree of compactness specified by the boundary length modifier of MARXAN. The degree of compactness is arbitrary, unrelated to the requirements of any particular process and assumed to benefit population dynamics and other processes and to facilitate management [37]. Figure 1b shows differences between two sets of high-priority areas, one with irreplaceability incorporating generic

design, the other with irreplaceability ignoring design. Each set contains the 200 areas with highest combined irreplaceability and threat values in the region. This addresses expanding threats by scheduling earliest conservation action for areas that are most likely to lose their forest types (high threat) and are difficult or impossible to replace if their forest types are lost (high irreplaceability). Previous applications of this method, further justification and limitations are discussed by Pressey *et al.* [6]. The two sets of priorities illustrate difficult tradeoffs between pattern and process. Priorities based on generic design (red, purple and pink areas combined) provide conservation managers with a more spatially coherent solution than priorities ignoring design (green, purple and pink areas combined). This benefit comes with the cost of excluding green areas with forest types that are more at risk from further clearing than those in red areas and for which larger percentages of remaining extents (up to 100%) are needed to achieve regional targets.

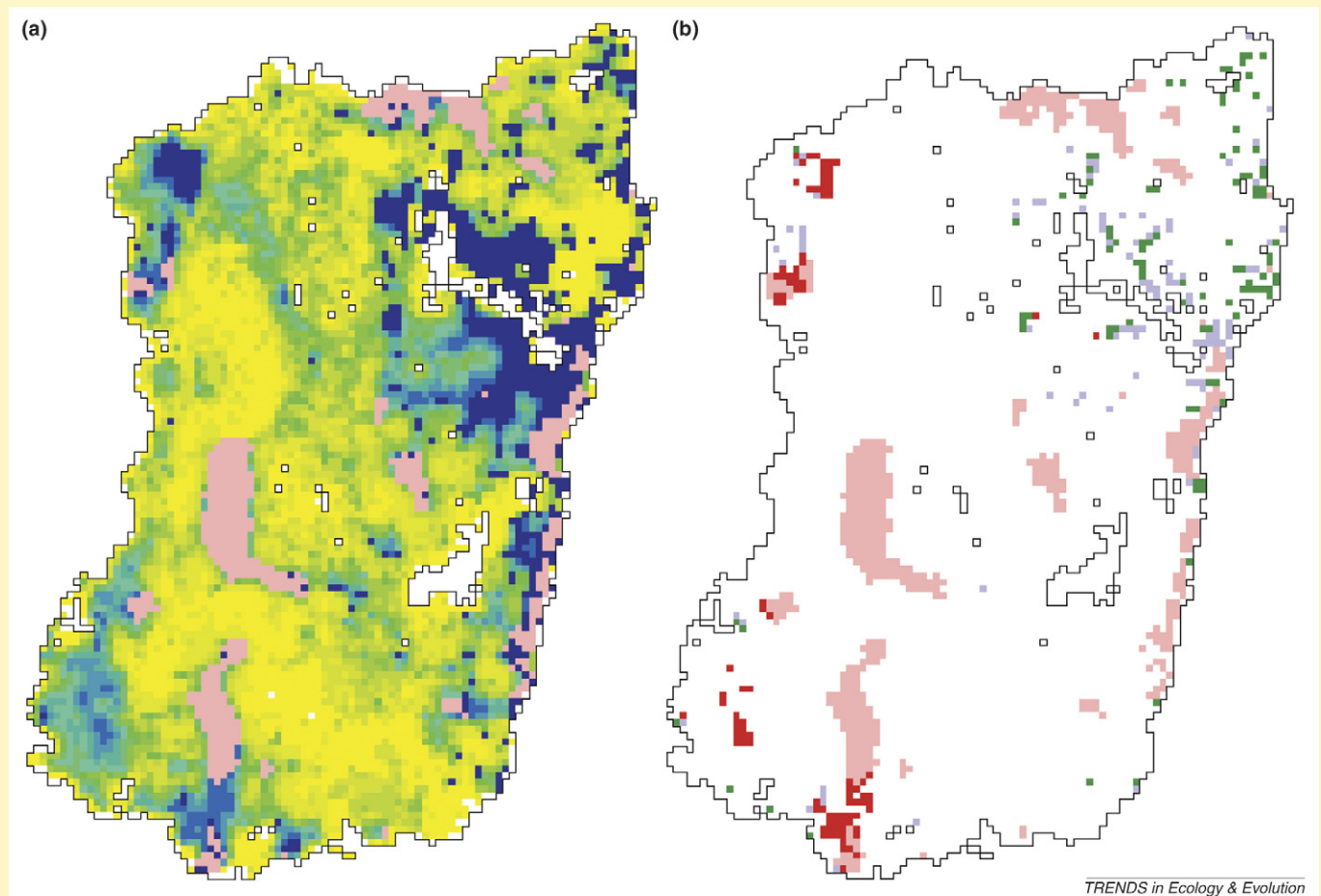


Figure 1. Options for conservation in north-eastern New South Wales. **(a)** Irreplaceability of areas. Pink areas are established reserves, whereas other colours show variation in the irreplaceability of areas, grading from yellow (low) to dark blue (high). **(b)** Different priorities for scheduling conservation action. Pink areas are established reserves. Purple areas have high priority regardless of whether whether irreplaceability considers generic design. Green areas have high priority only when irreplaceability ignores design. Red areas have high priority only when irreplaceability considers design.

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because of the lack of information about the quantitative design requirements of all but a few processes and the difficulties of planning for multiple processes simultaneously. Objectives for generic criteria involve statements of preferences, such as ‘bigger is better’, ‘balance representation with compactness’, or ‘where there is a choice, maximize connectivity between conservation areas’. Recent innovations for conservation planning have come from software tools that help to apply generic design

criteria, either by automatic selection of areas [37] (Box 2) or interactive use of decision-support systems by planners [28] or groups of stakeholders [38]. Specific design criteria[‡] are uncommon but used increasingly in conservation

[‡] Specific criteria for connectivity have been described as either ‘potential’ or ‘actual’ [35]. Potential connectivity metrics combine physical attributes of the landscape with limited information on the dispersal ability of species. ‘Actual’ connectivity metrics are informed by observations of individuals moving into or out of patches or through the landscape.

planning. Examples are minimum numbers of individuals to be represented in single conservation areas [39] and species-specific measures of connectivity [40]. The demands for data are greater [35], and typically only one or a few species or processes are involved. Interactive use of software to achieve specific design criteria is possible but can be tedious for multiple species or processes [39]. Special-purpose software to select areas automatically for specific design criteria [40,41] is therefore useful and represents another innovation.

These four approaches can be integrated (Box 3). After this, planners are faced with the third question we posed earlier: how to choose between processes (and elements of pattern) when conservation resources are insufficient for all to persist in the face of dynamic threats? Design criteria generally require biodiversity pattern to be represented at a higher cost for the potential benefit of enhanced persistence of processes [42], so limited conservation resources can require planners to prioritize between aspects of pattern and process [1,43]. Tradeoffs might also be necessary

Box 3. Integrating approaches to planning for biodiversity pattern and process

Conservation planning can be described by steps that help planners to identify and sequence their tasks and decisions. The steps below are indicative and adapted from work on the Cape Floristic Region of South Africa [28]. They constitute part of a larger sequence [1,2] and have been selected to illustrate how data and decisions can be integrated for biodiversity pattern and process.

1. Define planning units (areas to be assessed and compared for inclusion in the regional conservation plan). Optionally, planning units can vary in configuration and size to incorporate the boundaries of targeted spatial catalysts.
2. Subdivide extensive elements of biodiversity pattern (e.g. vegetation types) with spatial catalysts that demarcate parts of the region with different biogeographical histories.
3. Record the number and extent of each element of biodiversity pattern (e.g. species records, subdivided vegetation types) and each type of targeted spatial catalyst in each planning unit. This enables assessment of planning units according to their simultaneous contributions to targets for multiple features.
4. Identify regional conservation targets for elements of biodiversity pattern and spatial catalysts, adjusting targets to promote the persistence of species dynamics and other processes.
5. If potential conservation areas for specific design criteria have been designed separately, and if this exercise was time consuming or spatial options were highly constrained, identify these areas and already established reserves as core parts of the regional plan (Figure 1) and record their contributions to targets for biodiversity pattern and spatial catalysts.
6. Map the options for achieving the remaining targets for elements of biodiversity pattern, spatial catalysts and specific design criteria, if the latter were not covered in the previous step. Where there are options for selecting areas to achieve these targets, use interactive or automated methods (or a combination) to consider generic design criteria such as compactness or proximity to established reserves.
7. Implement different types of moveable conservation areas, considering their feasibility and effectiveness relative to biodiversity processes of interest and the constraints imposed by ownership and extractive uses.

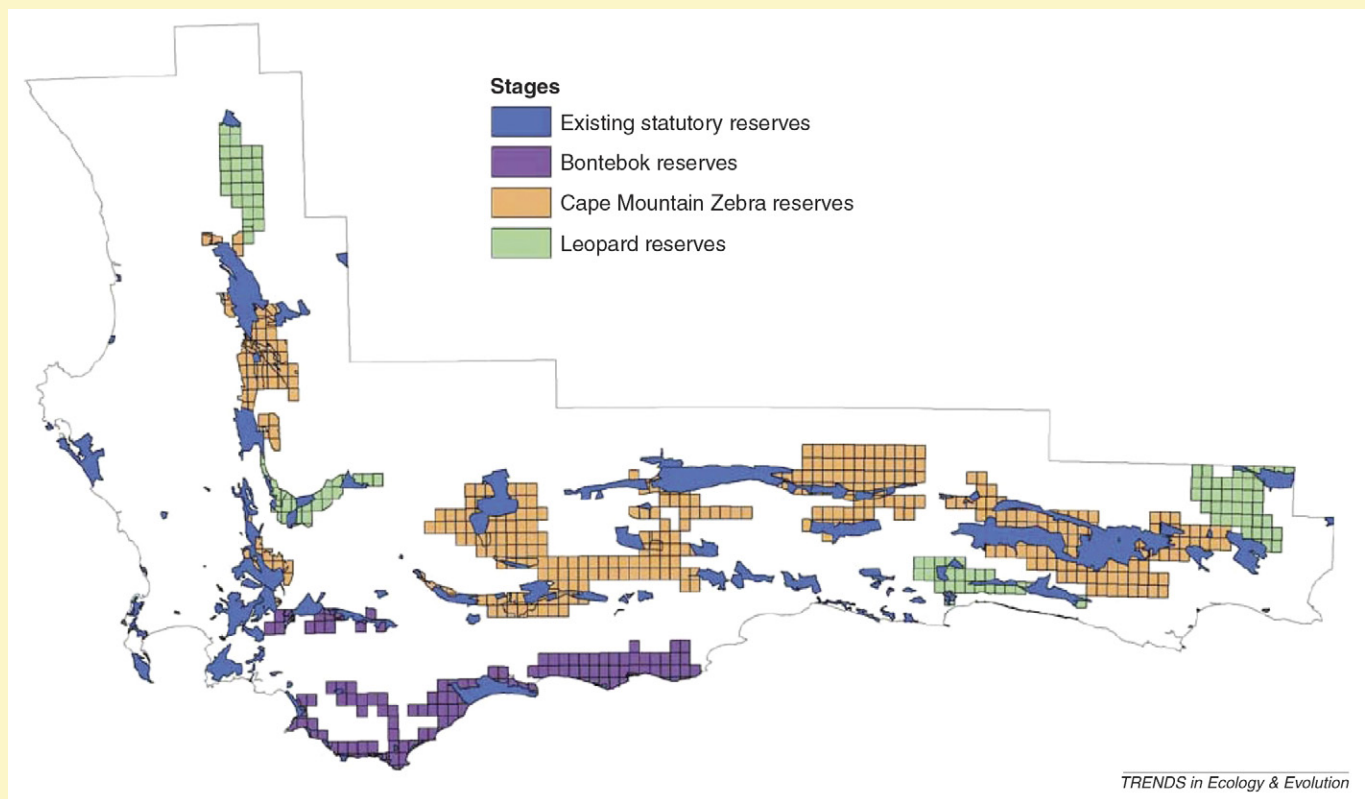


Figure 1. Areas designed interactively with planning software to achieve specific design criteria in the Cape Floristic Region [39]. For biological and management reasons, the criteria stipulated minimum numbers of individuals of 41 mammal species required in any single conservation area. Building on established reserves, the design focused sequentially on three species for which the criteria were most difficult to achieve (while also achieving them for other species): bontebok (*Damaliscus dorcas dorcas*), Cape mountain zebra (*Equus zebra zebra*) and leopard (*Panthera pardus*). Each grid square is about 39 km². Reproduced with permission from [39] and modified with permission from the senior author.

between different design criteria [44]. These are issues defined by Figure 1d and discussed below.

Planning for dynamic threats

Threats to biodiversity can be categorized as either ultimate or proximate [7,45]. Ultimate threats, such as increasing human populations and expanding global markets, are the root causes of biodiversity loss, operating at broad scales with social, economic and political origins. They are generally beyond the scope of conservation planning. Proximate threats are the localized expressions of ultimate threats, affecting biodiversity directly at regional or local scales. Among the most extensive and serious proximate threats to biodiversity are habitat conversion by agriculture, plantations or human settlements; harvesting of timber, fish and other natural resources; and invasive plants and animals. Conservation areas are effective responses to many, but not all [7], proximate threats.

Proximate threats are dynamic in three ways. First, they can expand or increase in intensity [45,46]. Second, they can contract or decrease in intensity [47,48]. Third, they can operate as spatiotemporal mosaics of impact followed by recovery, caused perhaps by altered fire regimes [49] or oil spills [22]. Dealing with dynamic threats requires planners first to predict spatially explicit changes in threats over their planning horizon [7], then to devise responses. Predictions come from statistical, process-based or expert-derived models [7,50–52]. We summarize here the responses concerned with retaining biodiversity pattern in the face of threats (Figure 1c).

Expanding threats

Attention has focused on planning responses to expanding threats, which are the most important causes of biodiversity loss [45,53,54]. Planners can address these throughout the planning process [7] but we consider three compatible approaches: (i) adjusted representation targets; (ii) locating threat-specific actions; and (iii) scheduling conservation action. Larger targets have been recommended for more threatened biodiversity features [9,21,22]. The rationale is straightforward: occurrences of these features are less likely to be retained outside conservation areas, so more should be inside. This approach has been criticized [3] but the alternative is potentially problematic. For example, threat-free targets under the South African Biodiversity Act will probably produce uneven retention of ecosystems with the same levels of species heterogeneity and require special applications for endangered status to limit this imbalance.

Effective conservation should involve a variety of threat-specific conservation actions. Strict reservation is not always sufficient or necessary. Other appropriate actions within or outside reserves include control of invasives, management of disturbance regimes, quarantine against disease, restrictions on harvesting, and restoration. With few exceptions [55,56], studies in systematic conservation planning have not allocated or coordinated multiple actions. Where there are spatial choices for applying actions, choosing areas that are less exposed to expanding threats has the advantages of minimizing conflicts with development, reducing management liabilities arising

from outside pressures and perhaps reducing conservation costs [19,28,57]. Then, decisions about the boundaries of conservation areas can limit intrusions from existing threats and provide insurance against expanding ones. Alignment with catchment boundaries is often important [36], as are criteria such as shape and size which influence buffering of areas from outside threats [58,59].

Scheduling concerns the sequence in which areas will be given protection (Box 4). Limits on conservation resources mean that new conservation areas are typically implemented incrementally, even if they are part of a regional plan. During this protracted process, expanding threats continue, destroying or reducing the value of some areas that are important for conservation. In this context, scheduling is important because it determines the extent to which conservation targets are compromised by dynamic threats [6,28]. Methods for scheduling for biodiversity pattern have had two objectives: (i) maximizing gain (considering only what is inside conservation areas) [60]; and (ii) minimizing loss (considering what is retained both inside and outside conservation areas) [6]. Within regions, minimizing loss is preferable when spatial variation in threat is large [61] and confidence in that predicted variation is sufficient to justify decisions. Loss is then minimized by directing limited resources away from unthreatened areas and toward more threatened ones with fewer replacements for achieving conservation targets [1,62]. Notably, conservation outcomes are poorer if expanding threats are ignored than when they inform decisions about scheduling [6,60].

Contracting threats

Threats can contract passively following depopulation of rural regions and subsequent afforestation. Effects on biodiversity can be positive for some species but negative for others [47], representing an expanding threat for the second group. If patterns of regrowth can be anticipated, they could influence planning decisions, perhaps augmented with active intervention to influence structure and composition. Contracting threats might arise from active restoration with ecosystem services as the primary objectives, including carbon sequestration and soil conservation. This involves the risk that high potential values for biodiversity will be missed by restoration for other objectives [63]. With spatial data on restoration value for multiple objectives, including biodiversity, planners can capitalize on spatial congruence between high values and develop approaches to negotiate spatial divergence, including multicriteria methods for locating investments [64]. A third aspect of contracting threats involves opportunities for restoration specifically for biodiversity pattern, perhaps to reverse the depletion of some habitat types. Ideally, this restoration would be configured to benefit biodiversity processes [9] (Figure 1d).

Threats as spatiotemporal mosaics

Threats operating as spatiotemporal mosaics vary from those with few or no prehuman analogues, such as oil spills [22] and deep-water trawling [51], to those resembling prehuman disturbances but altered in specific impacts and timing, such as anthropogenic fire [49], slash-and-burn

Box 4. Making decisions with dynamic conservation priorities

Scheduling or sequencing of conservation action is necessary in the common situation where limited resources require conservation action to be applied incrementally while unprotected areas remain at risk of losing their biodiversity values [6]. Careful choices between areas are then needed in time as well as space. A framework for scheduling conservation action in relation to irreplaceability and threat [6,78] is an initial guide to priorities, expressed as a list or map. Alternatively, optimal or near-optimal sequences of conservation investments can be identified [61,62]. These schedules, however, need regular updating. Progressive conservation action reduces the irreplaceability of some unprotected areas because of complementarity between areas in the biodiversity features that they contain [1]. Expanding threats reduce the biodiversity and therefore irreplaceability of some areas but increase the irreplaceability of others that become more important for achieving conservation targets [1]. Threats to particular areas change through time [7]. Similarly, optimal or near-optimal sequences need updating as areas are protected and lost and the relative conservation values and threats of remaining areas change [62].

Updating of conservation schedules would ideally involve dynamic interaction between special-purpose software for both conservation planning and modelling future threats (Figure 1a) but we are not aware of such an approach being applied. A challenge for modelling threats concerns negative and positive feedbacks. Conservation action can reduce threats, perhaps by eliminating sources of weed invasion, or increase them by displacing development pressure to previously unthreatened areas [67]. Other, barely explored issues include scheduling in relation to varying costs of areas [57,61] and their availability for conservation action [60,61].

Dynamic updating of priorities for both biodiversity pattern and process makes this picture considerably more complex (Figure 1b), highlighting the potential for interacting models to inform conservation decisions. Expanding threats change the quality and connectivity of patches of habitat, affecting species persistence (process 1) [79]. Conservation action alters the proximity of unprotected areas to established conservation areas and their contributions to compactness [37] (process 2). Anticipated changes to species distributions with climate change [18] (process 3) and simulations of patch dynamics [49] (process 4) will influence decisions about conservation design, and so on. The models that help to understand processes will also interact among themselves [71]. Predictions of climate change, for example, will alter predictions of threats such as expanding weeds and agriculture, influence the expected persistence of species in some areas, and change the projected dynamics of fire.

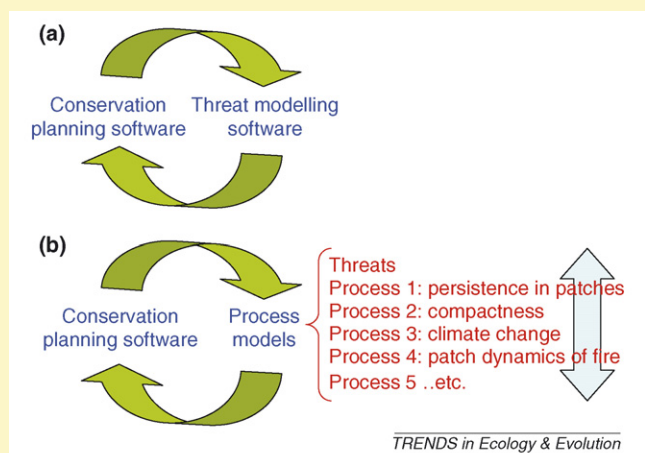


Figure 1. Interacting software systems to guide decisions about scheduling conservation action. **(a)** Dynamic conservation priorities for biodiversity pattern. **(b)** Dynamic conservation priorities for biodiversity pattern and process.

agriculture and logging [24]. Not surprisingly, some of the planning responses are similar to those for 'natural' [20] patch dynamics: moveable conservation areas to encourage appropriate management of postdisturbance phases [24] and adjusted conservation targets to account for the expected impacts from dynamic threats [21,22]. Active intervention in anthropogenic disturbance regimes might be necessary both within and outside areas managed for conservation [52,65], depending on the effectiveness of conservation areas in mitigating their impacts. The boundaries of protected areas are permeable, for example, to altered regimes of fire and flooding.

Uncertainty about threats

Prediction of threats always comes with uncertainty arising from errors in data [66], limited understanding of the sources of threats [7], stochastic factors such as decisions by individual landholders, feedbacks between conservation action and threats [67], unexpected combinations of threats [68] and novel threats that are difficult to predict [46]. Underlying these limitations is the potential for larger uncertainties caused by changes in ultimate threats. Government policies that push people into the forest frontiers of developing countries, for example, can cause escalations of proximate threats [45]. Conceivably, predictions of threats could be so uncertain that they are not useful. This potential is mitigated by the extensively demonstrated dependence of threats on environmental variables, proximity to infrastructure, sources of invasive weeds, and other factors [7]. Nonetheless, uncertainties require more attention from planners. Responses to uncertainty include identifying plausible bounds to predictions [69], precautionary decisions that avoid underestimating threats, regular revisions of predictions [7], alertness for novel threats and scenario modelling [70,71].

Planning for biodiversity processes and dynamic threats

The intersection of natural and anthropogenic dynamics (Figure 1d) combines the complexities of both, highlighting the gaps between available and required techniques for adequate planning responses. This combination of dynamics has received little attention in the literature on systematic conservation planning, although work in related areas has contributed. An overarching issue is climate change, simultaneously a driver of processes of range adjustment, having operated throughout the history of the planet, and a dynamic threat. Anticipated rapid anthropogenic changes in climate are likely to reduce or eliminate habitable space for many species, exacerbated by transformed landscapes that will impede range adjustments [72]. Work has begun on conservation design to facilitate these adjustments [18,19] but uncertainties remain about the effectiveness of alternative approaches. Effective process-related responses to climate change and other dynamic threats also require information on population sizes that are necessary to maintain sufficient genetic variability for adaptation [5,12] and might involve recognizing, maintaining or avoiding contemporary adaptations of some species to anthropogenic changes [5,16].

Contracting threats offer opportunities for passive or active restoration to favour the persistence of biodiversity processes, or might indicate the need for management to avert declines of valued, open-country species, such as certain species of songbirds [47]. Methods are being developed for configuring restoration actions to improve design [29,73] and scheduling incremental investments in restoration for design [74]. These can guide actions specifically for biodiversity or contribute to multiobjective programmes. Climate change requires restoration objectives to depart from purely historical references [75] and to include adjustments of the ranges of species [19].

The influence on biodiversity processes of threats operating as spatiotemporal mosaics has been widely recognized [21,24]. A remaining challenge for conservation planning now being addressed [76,77] is to evaluate the different disturbance regimes arising from alternative policies and management prescriptions by linking models for landscape simulation and species persistence. These combine the advantages of spatial explicitness, temporal dynamics and estimation of uncertainty to guide conservation design and changes in management.

Scheduling conservation action with expanding threats is more complex when biodiversity processes are involved. Scheduling for biodiversity pattern has been adapted for the persistence of space-demanding animals such as large carnivores [78] but, ideally, progressive scheduling decisions involve dynamic updating of threats and conservation priorities for multiple aspects of pattern and process. This synthesis is demanding (Box 4) and has not been addressed comprehensively, although parts of the picture have been filled in. Examples are modelled interactions between expanding threats and priorities for metapopulation persistence [79] and scenarios of interacting climate change, threats and conservation areas [71]. Biodiversity processes add further complexity to scheduling when many areas are irreplaceable and highly threatened. Choices about which areas and features to protect are then also choices about which areas and features will be lost (Box 2). Explicit methods for choosing between multiple aspects of biodiversity pattern and process are needed [1,28,43] but are currently unavailable. Scheduling for conservation design is a case in point [42,44]. Rapid implementation of an entire configuration reduces its risk of being compromised before completion but diverts resources from elements of pattern [4] that might be lost regionally or globally.

Concluding comments

Conservation planning in a changing world involves three broad challenges. First, biodiversity processes always need attention, regardless of whether they are explicitly recognized [80]. Second, most planning situations involve dynamic threats, regardless of whether they are considered [6]. Conservation decisions that ignore natural and anthropogenic dynamics can be relatively ineffective in promoting the persistence of biodiversity but are made daily. More effective conservation planning depends partly on science catching up with these two aspects of a changing world. A third challenge involves practice catching up with science. Many practitioners are adopting systematic

methods and acknowledging the roles of software in analysis and decision support [2,3] but many remain distant from modern planning tools, either by choice or circumstance. As science deals better with dynamics, more computer models will become involved (Box 4) and it will be increasingly important for practitioners to be kept abreast of new methods while also validating their utility. The risks are that practitioners will find ever more complex models impenetrable and irrelevant and that the present gaps between science and practice will widen. Reversing this trend requires scientists to take on additional roles [3]: communicating more effectively with practitioners and other stakeholders; explaining science more transparently; and engaging in long-term collaborations to promote effective implementation.

Acknowledgements

The title of our review is a slight variation on that of an important book [80] which encouraged conservation biologists to consider dynamics and influenced the ideas in this article. We thank Lauren Cave, Graham Kerley and Carissa Klein for data and help with analyses. R.L.P. acknowledges support from the ARC and CERF (Applied Environmental Decision Analysis). M.C. acknowledges support from the Academy of Finland, Project #209017 and EU FP6 project MACIS (N°044399, www.macis-project.net). R.M.C. acknowledges support from the NRF. Three reviewers improved the paper.

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