Managing climate-change refugia to prevent extinctions

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Managing climate-change refugia to prevent extinctions

Gunnar Keppel[1,2,*,@], Diana Stralberg[3,@], Toni Lyn Morelli[4,@], and Zoltán Bátori[5,6,@]

Earth is facing simultaneous biodiversity and climate crises. Climate-change refugia – areas that are relatively buffered from climate change – can help address both of these problems by maintaining biodiversity components when the surrounding landscape no longer can. However, this capacity to support biodiversity is often vulnerable to severe climate change and other stressors. Thus, management actions need to consider the complex and multidimensional nature of refugia. We outline an approach to understand refugia-promoting processes and to evaluate refugial capacity to determine suitable management actions. Our framework applies climate-change refugia as tools to facilitate resistance in modern conservation planning. Such refugia-focused management can reduce extinctions and maintain biodiversity under climate change.

Highlights

Climate-change refugia can support biodiversity by maintaining buffered conditions despite climate change and are a critical tool for the unfolding extinction crisis.

Despite their capacity to protect biodiversity, climate-change refugia will be increasingly vulnerable to the impacts of multiple interacting stressors and may hence require management.

Effective protection of biodiversity under climate change can be facilitated by managing or newly establishing climate-change refugia on the basis of multiple factors and processes that create them.

Using four clear steps, appropriate actions to maintain climate-change refugia, ranging from minimal management to more extensive restoration efforts, can be determined.

Identifying and managing climate-change refugia can reduce extinctions and contribute to landscapes that are holistically managed for biodiversity conservation under climate change.

Refugia as safe havens

Earth is heading toward a sixth mass extinction event [1]. While the current **extinction crisis** (see Glossary) is driven mainly by land-use change, overharvesting, and biological invasions, climate change is becoming a major contributor to extinction and is exacerbating existing drivers [2,3]. Extinctions can cause cascading effects that alter ecosystem structure and functioning [1,4].

Climate change impacts are increasing in severity, and reversal is becoming unlikely, driving a paradigm shift in landscape conservation toward promoting climate-change resistance in low-vulnerability areas and facilitating inevitable transitions in more vulnerable areas [5,6]. In this context, **climate-change refugia** are seen as climate-resistant bastions [7–9] that remain relatively buffered from the effects of climate change. They constitute areas that biodiversity can retreat to and persist in [10,11], thereby facilitating persistence during periods of climate change [12,13]. As such, climate-change refugia are potential 'safe havens' for maintaining biodiversity under anthropogenic climate change and for abating the unfolding extinction crisis [8,14,15].

However, refugia must be integrated with other management considerations [7,10] and may have limits to how much climate change they can buffer [8,9,12,16,17]. Thus, it is important to understand the factors and processes that affect refugia function and quality and to prioritize areas for conservation that are likely to persist for longer time periods [15,17,18].

Here we first develop a conceptual model of the biological and physical factors that affect climate-change refugia. We then build on the concept of **refugial capacity** to illustrate how it can assist in identifying the most buffered and most persistent (i.e., long-term) safe havens for biodiversity. We highlight how managing climate-change refugia as complex and dynamic systems that are affected by **global change** is key to conserving them. Finally, we integrate these considerations into a conceptual framework of **refugia-focused management** that extends to the restoration of urban and degraded habitats.

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Multidimensionality of refugia

Refugia are multidimensional habitats (Figure 1); multiple metrics may therefore be required to identify them and understand their functioning [8,19–21]. Initial studies of climate-change refugia centered on their size, location, and persistence through time [18,22]. **Climate velocity**, which represents the speed at which species must migrate to maintain constant climate conditions [23,24], has been used to identify areas that are less exposed to climate change [15]. However, climate velocities do not consider fine-scale physical factors, such as microtopography and soil type, and biological factors, such as ecosystem engineers [e.g., beavers (genus *Castor*) and peat mosses (genus *Sphagnum*)] and microclimate modifiers (e.g., forest canopy). These **biophysical factors** promote processes that facilitate the formation and maintenance of climate-change refugia (i.e., **refugia-promoting processes**) [17,25–30]. For example, water cycling in swamps and peatlands, aided by peat mosses, can maintain persistent moisture that locally reduces the frequency and intensity of fires and droughts, which are increasing due to climate change [17,27]. In addition, the multitude of climate **stressors** from which climate-change refugia provide shelter, such as drought and heat, needs to be considered [31]. Additional stressors from other anthropogenic disturbances, such as habitat conversion and pollution and their interactions with each other and climate stressors, are increasingly being considered alongside climate-change refugia [21,32,33].

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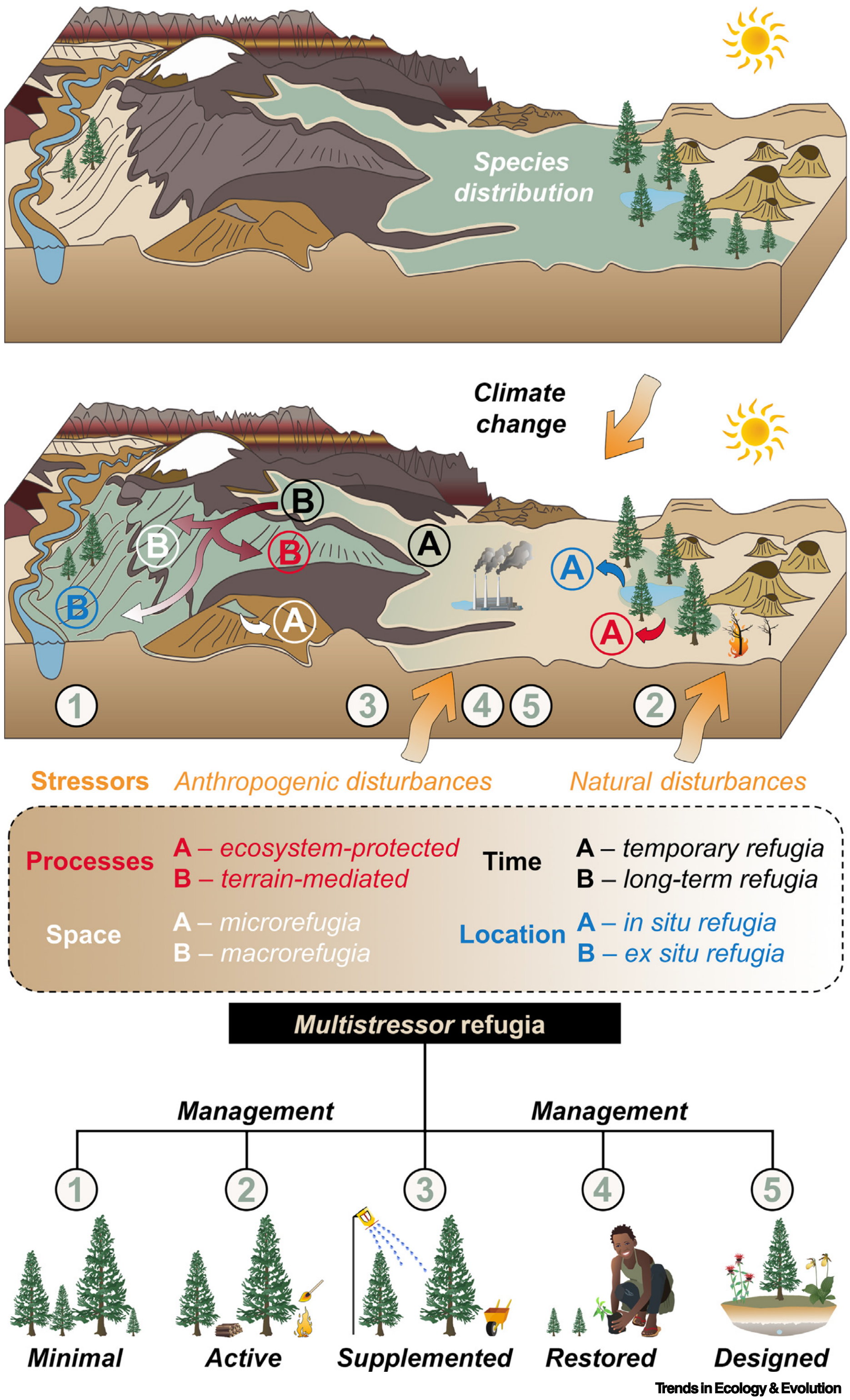
We suggest that climate-change refugia can be conceptualized across four dimensions: space, time, refugia-promoting processes, and stressors (Figure 1). Refugia-promoting processes will vary in space and time, defining the size and location of climate-change refugia. Because species display unique responses in this multidimensional space, refugia are principally species- and stressor-specific [18,34]. However, climate-change refugia can protect multiple taxa whose distributions are influenced by similar **biophysical thresholds** [7–9,26,34,35].

The emergence of stressors can instigate changes in refugia-promoting processes. For example, partial drainage and more intense droughts can reduce the moisture retained in peatlands [36]. Beyond certain biophysical thresholds, refugia-promoting processes will be affected, reducing the **buffering** capacity of climate-change refugia. For example, aridity thresholds have been linked to three stages of decline – reductions in (i) productivity, (ii) soil fertility, and (iii) vegetation cover – leading to the eventual collapse of ecological communities [37]. Thresholds are therefore key to understanding ecosystem decline and can provide important indicators for managing climate-change refugia as dynamic, multidimensional habitats affected by multiple stressors. However, thresholds are not always clearly identifiable [38] and can be difficult to quantify [39]. Furthermore, thresholds at which refugia-promoting processes cease to effectively buffer ecosystems from climate change are generally not known [19,40].

Refugia-focused management

We define refugial capacity as the ability to facilitate the long-term persistence of taxa, which is dependent on providing buffering from climate change and other ecological requirements to support viable populations [8,30]. To persist, a population requires the survival of adult individuals, reproductive success, and interactions essential to survival and reproduction [27]. Therefore, the performance of a population and its key intra- and interspecific ecological interactions need to be considered when evaluating the likely effects of climate change. Biophysical thresholds and their likelihood of being exceeded under climate change may be integrated into a measure of capacity. Although the potential of a quantitative approach for assessing refugial capacity is apparent [8], a suitable, widely accepted methodology is lacking.



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Glossary

Anthropogenic refugia: climate-change refugia that were created by human activities (e.g., abandoned mine shafts that provide cooling and retain water). They can be created unintentionally or designed (e.g., creating shaftlike depressions to provide cooler and moister microclimates).

Biophysical factors: biological (e.g., ecosystem engineers and microclimate modifiers) and physical (e.g., microtopography and soil type) factors.

Biophysical threshold (of a refugium): a point beyond which a refugium can no longer maintain an environmental condition important for the persistence of a population or an ecological community in the face of climate change, which equates to a point beyond which it loses some or all of its buffering capacity.

Buffering (climatic): the moderation of changes in climatic conditions through time by the physical environment (e.g., moderation of heat stress on pole-facing slopes) and biological processes (e.g., heat stress moderation by canopy). The physical and biological drivers of buffering may also protect from extreme climatic events.

Climate velocity: the speed and direction at which species must migrate to maintain constant climate conditions. For example, an increase in annual mean temperature could require a population to migrate 1.0 km year^{-1} poleward to retain current climate conditions.

Climate-change refugia: areas that are relatively buffered from contemporary climate change over time and where biodiversity can retreat to and persist in.

Designed refugia: a type of anthropogenic refugia, which are specifically designed to buffer climate change sufficiently to support selected taxa and refugia-promoting processes.

Disturbance regime: the temporal and spatial dynamics of natural and/or anthropogenic disturbances, and their interactions, that are affecting a landscape over a longer period, with disturbances being discrete events that temporarily or permanently alter the functioning and structure of ecosystems.

Extinction crisis: the rapid loss of biodiversity that our planet is currently experiencing, including the loss of genetic, taxonomic, and ecological diversity with profound consequences for ecosystems and humanity.

We propose that management priorities for climate-change refugia can be identified using four steps: (i) identifying target taxa and regions, (ii) researching biophysical thresholds, (iii) estimating refugial capacity, and (iv) deciding on management actions (Figure 2). First, taxa or ecological communities considered vulnerable to climate change are identified on the basis of best available information about their climatic exposure (e.g., niche model projections) and sensitivity (e.g., life-history traits) [10]. Next, the key physical and biological requirements and, if possible, their thresholds are identified. For example (Figure 2), an isolated population of red stringybark (*Eucalyptus macrorhyncha*) in South Australia [16] was assessed as genetically distinct and vulnerable to the effects of climate change (step 1). Prolonged drought and extreme heat have been identified as key drivers of widespread dieback (step 2). Next, the known or suspected factors influencing persistence of the population can be integrated using process-based modeling [44] or other approaches to estimate refugia management potential across the landscape, which, for the red stringybark, is highest on pole-facing aspects [16], away from the warmest solar radiation and hot, northwesterly winds (step 3).

Refugial capacity can hence indicate the management requirements of climate-change refugia and provide specific information about their quality and long-term persistence (Figure 2). The final step uses this information to derive management actions for prioritized refugia. For the *E. macrorhyncha* population (Figure 2), targeted irrigation of **pole-facing slopes** with the highest refugial capacity under extreme weather conditions could alleviate drought stress (step 4), expanding the capacity of the refugium by maintaining water cycling processes. This four-step refugia-focused management approach hence maximizes the chance of conservation success and can be implemented at a range of scales.

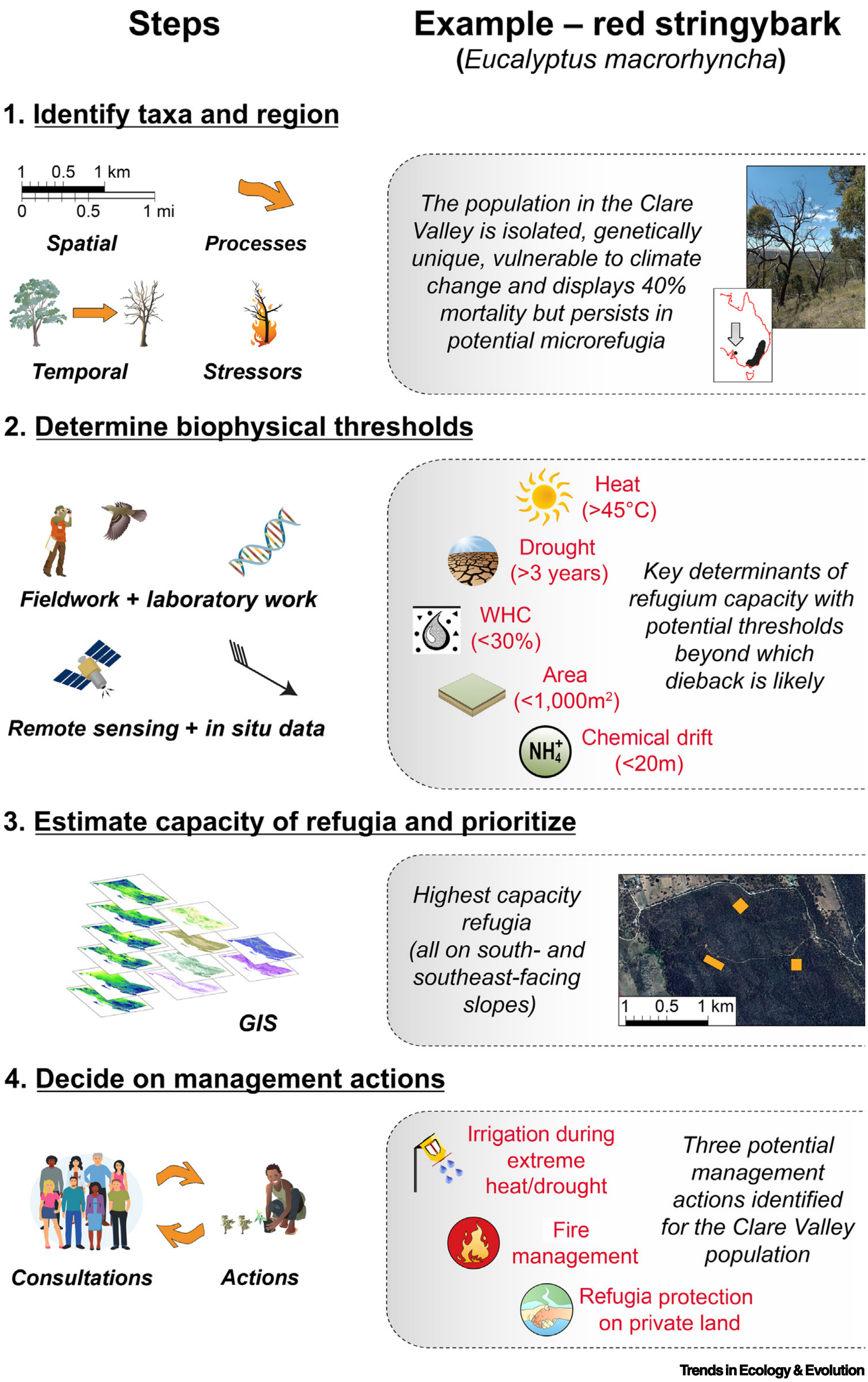
Management of climate-change refugia

Although refugia have generally been the target of conservation efforts (e.g., [21,45]), active management may be required to retain their capacity to support biodiversity (Figure 1, [46]). This is reinforced by a growing understanding that very few, if any, ecological systems are untouched by humans and that activities of Indigenous peoples over millennia have influenced the current distribution of species [22].

Different levels of climate-change refugia management may be required (Figure 1), depending on the magnitude and rate of climate change [22], the landscape setting, the refugial capacity, and the taxa involved. Landscape setting is particularly relevant in highly modified landscapes, where species may be more vulnerable to extinction [47]. High-capacity refugia in relatively intact landscapes may require minimal management, as they can strongly buffer climate change. For example, deep topographic depressions can be strongly decoupled from regional warming because of the pooling of cooler, heavier air [48]. Refugia that are maintained by weaker buffering

Figure 1. Managing climate-change refugia on the basis of refugia-promoting processes. For a given species distributed across a landscape (top panel), the locations of climate-change refugia are determined by different refugia-promoting processes across space and time. Refugia locations may be affected by multiple stressors, including climate change; other anthropogenic disturbances, such as habitat conversion; and natural disturbances, such as fire (middle panel). Previously proposed typologies of refugia referred to refugia-promoting processes (ecosystem-protected versus terrain-mediated mechanisms [19]), space (microrefugia versus macrorefugia [41]), time (long-term versus temporary refugia [42]), and location (*ex situ* versus *in situ* refugia [43]). Management may be required to maintain climate-change refugia and requires integrated knowledge of refugia-promoting processes and stressors. Management can be minimal, active (e.g., controlled burns), or supplemented (e.g., irrigation) or may involve restoring or designing refugia (bottom panel). Images are from the Integration and Application Network (http://ian.umces.edu/symbols/) and https://publicdomainvectors.org/.

Global change: changes in the Earth's system due to human activities that are affecting ecosystems globally. It hence includes various stressors, such as warmer temperatures due to climate change and more fragmented vegetation due to habitat conversion.
Microrefugia: small areas that provide favorable conditions not available in the surroundings and can facilitate the long-term persistence for a taxon in the landscape, with 'small' being relative to the taxon or community under consideration and opposed to larger, continuous extents of area ('macrorefugia').
Pole-facing slope: a slope that faces in the direction of the closest pole, being south in the Southern Hemisphere and north in the Northern Hemisphere, and hence receives less solar radiation and heat loading.
Refugia-focused management: approach that prioritizes identifying and managing refugia to retain biodiversity under climate change.
Refugia-promoting processes: biophysical processes that facilitate the formation and maintenance of climate-change refugia.
Refugial capacity: the potential of refugia to facilitate species persistence under climate change, which is determined by the ability to provide suitable conditions for healthy populations. It will differ among sites and is specific to a species, a group of species, or an ecological community.
Stressor (biophysical): a biological or physical factor that negatively affects the health of a population or ecological community, such as lower water ability due to more severe droughts.



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processes (e.g., limited topographic shading) may require intervention to maintain, especially in heavily modified landscapes ('active' in Figure 1).

Active management may be particularly relevant for climate-change refugia susceptible to natural disturbances, which influence the distribution of ecological communities and species. **Disturbance regimes** may be altered by climate change or may interact with other stressors (e.g., warmer temperatures) to catalyze ecosystem transitions [49–51]. For example, wildfires are becoming more severe in many systems [35,51], threatening current climate-change refugia, as hotter and drier conditions reduce their ability to buffer against wildfires [20,35,46]. These more severe fires may be managed by identifying biophysical characteristics that reduce their likelihood and by fuel management through thinning or prescribed fire [52,53]. Longtime practices of Indigenous peoples, such as cultural burning, can inform or guide management plans for highly dynamic systems [51]. However, if specific biophysical thresholds are exceeded, such as moisture retention in peatlands becoming too low to retard fire, management may require supplementing refugia-promoting processes by actions such as irrigation or physical protection ('supplemented' in Figure 1).

A mechanistic understanding of what causes and maintains refugia, and how these factors will be affected by climate change, is key to effective management. Some terrain-mediated processes, such as orographic and hydrologic effects, have been well studied [17,48]. Buffering driven by biological factors is less well understood and can be more transient. For example, vegetation cover is known to buffer temperature [34,54,55], but research is only beginning to identify the biophysical thresholds at which vegetation structure changes [37]. Furthermore, many refugia-promoting processes are directly threatened by climate change, creating uncertainty about their long-term effectiveness. For example, inland penetration of coastal fog near regions of off-shore upwelling creates locally cooler conditions that may serve as climate-change refugia [10]. Recent data indicate that climate change is affecting fog formation and may diminish this buffering rapidly [56]. Better understanding of how refugia-promoting processes will be affected by climate change is needed (see Outstanding questions).

However, even after biophysical thresholds are exceeded and a relatively buffered habitat ceases to be a safe haven for one species, a refugium may still be valuable for other, more tolerant, taxa that benefit from the climate buffering [15,30,57]. For example, when the more shaded, pole-facing slopes become too warm for the currently supported taxa [58], they may still support species that were displaced from more exposed sites. This transient nature of refugia is important to consider in decision-making [15]. Planning for species turnover in and among refugia could

Figure 2. Applying refugia-focused management. On the left, the four major steps of the process are provided. On the right, an example based on an ongoing project investigating dieback in an isolated population of the red stringybark tree (*Eucalyptus macrorhyncha*) in the Clare Valley, South Australia, is provided (see [16] for more details). In step 1, the population was identified as being vulnerable to drought, based on dieback of trees (temporal consideration) and being restricted to a small area (spatial consideration). Potential changes to refugia-promoting processes or stressors could also be used to identify taxa or ecological communities to target for conservation. In step 2, field and laboratory studies, using both *in situ* and remote sensing data, found that prolonged drought (below average rainfall in three consecutive years), extreme heat (exceeding 45°C), and low soil water-holding capacity (WHC, below 30%) were related to adult mortality. Drift of chemicals associated with viticulture (<20 m from the forest edge) and the area of healthy vegetation remaining (<1000 m^2) could be additional stressors. Note that the biophysical thresholds provided (in brackets) are inferred, with research ongoing. In step 3, these thresholds can be integrated using various approaches (e.g., [44]) that can estimate the capacity (to support target taxa/communities under climate change) of refugia and to ultimately prioritize the refugia with the highest capacity. Management actions can then be determined in consultation with land managers and other stakeholders (step 4). Images are from the Integration and Application Network (http://ian.umces.edu/symbols/) and https://publicdomainvectors.org/. Photo: G.K. Base Map: Google Maps. Abbreviation: GIS, geographic information system.

improve the outcomes of integrating refugia into conservation management but adds further complexities (see Outstanding questions).

Finally, there are long-term risks to climate-change refugia. For example, refugia could become isolated oases in hostile landscapes that prevent dispersal in or out, creating island-like conditions. An isolated population may become evolutionarily or ecologically differentiated from other populations [59,60], which could affect its adaptability to climate change. Similar to islands [61], refugia are also unlikely to receive the full complement of species from their source communities, which could affect key ecological relationships. This could have far-reaching consequences and influence community responses to global change [62]. As climate change progresses, these long-term effects will become increasingly relevant and will need to be appropriately managed (see Outstanding questions).

Establishing refugia in degraded landscapes

In heavily developed or degraded landscapes, where refugial capacity is more limited, there may nonetheless be opportunities to manage and restore refugia for both ecological and societal benefit. For example, restoration could be focused on places that are potential refugia [32,63] because of their physical settings ('restored' in Figure 1), such as sites that are hydrologically or topographically buffered. Such buffering could provide protection for plants at their most vulnerable stages as seedlings and hence could increase the success of some restoration activities.

In-depth knowledge of species' biophysical requirements and refugia-promoting processes would allow refugia to be designed and established in new locations (Figure 1). Indeed, some climate-change refugia have been inadvertently designed by past human interventions. For example, likely as a result of 20th-century warming, the climate-sensitive Belding's ground squirrel (*Urocitellus beldingi*) has been extirpated from most low-elevation sites in eastern California, except in a county park with regular lawn irrigation that mimicked some aspects of natural meadow conditions [60]. In Hungary, some topographic depressions in drying, sandy lowland areas created by mining activities now provide refugia for several species requiring moister conditions [64]. Although such **anthropogenic refugia** [60] arose as unintentional by-products of human activities, they could also be intentionally designed to support biodiversity under climate change (**designed refugia**). Logistically, the establishment of designed climate-change refugia is most feasible at smaller scales (i.e., as **microrefugia**), although they can also be implemented at larger scales if sufficient resources are available.

Harnessing synergies

Management actions need to integrate relevant socioeconomic and cultural considerations to achieve synergies and avoid unintended outcomes. For example, some potential refugia are located within protected areas, which may increase the feasibility for management actions [45,65]. However, most landscapes have an active human presence, which means that there are socioeconomic and cultural values to consider alongside ecological conservation. Traditional territories of Indigenous peoples have been managed for millennia using traditional knowledge and a holistic approach that is inextricably linked with cultural values [66]. Landscapes managed for resource extraction also offer opportunities for considering and managing refugia as part of regional land-use planning activities.

Fruitful synergies for biodiversity conservation and climate-change adaptation may arise in urban, suburban, and industrial development settings, where drought and heat stress may be more easily managed [21,67,68]. Furthermore, the consideration of refugia could also provide broader societal benefits, such as natural flood protection zones and reforestation for carbon sequestration –

with climate-change refugia increasing the chances of long-term retention of sequestered carbon compared with less suitable locations [69]. However, there may also be trade-offs between climate-change adaptation (i.e., refugia conservation) and mitigation (i.e., carbon footprint reduction), especially in landscapes managed for resource extraction. Thus, navigating public perceptions, as well as economic and carbon considerations, will require careful planning (see Outstanding questions).

Concluding remarks

Biodiversity conservation is increasingly adopting the paradigm of either resisting climate change or facilitating unavoidable transitions [5], and refugia are a tool to facilitate resistance. Determining refugial capacity across landscapes could assist with identifying priority sites and guiding where to implement which approach. Practically, refugia are where critical biophysical thresholds of taxa are least likely to be exceeded and therefore offer the best chance of persistence for many taxa. While this is a tantalizing prospect, pathways to effectively identify and manage locations that will remain suitable for target species and communities within resource constraints need to be pinpointed first.

Appropriate management of refugia can avoid negative outcomes that may occur if the refugial capacity declines as climate change intensifies and therefore reduces the likelihood of extinctions. It will be important to consider the complexity of ecological responses that climate change and other disturbances may elicit, as well as their effects on refugial capacity. The framework for refugia-focused management presented here takes these complexities into consideration and can be applied across landscapes to identify areas with the highest refugial capacity. Therefore, managed refugia and the concept of refugial capacity constitute powerful tools to help abate the extinction crisis.

Outstanding questions

How will refugia-promoting processes be impacted by climate change? Answers will need to consider how biophysical factors will be affected and how this will impact these processes. Using the example of inland penetration by fog in the text, we will need to know how climate change will impact coastal currents and cold-water upwelling and how that would affect the frequency and amount of fog formation and how species are likely to respond.

How can we best integrate the transient nature of climate-change refugia in conservation planning? As a refugium becomes unsuitable for one taxon, it can still provide sufficient buffering from climate change to benefit other taxa. For example, managing a landscape that includes various interconnected refugia with different capacities may allow species to move between and persist in different refugia as climate change progresses.

How can we manage or harness long-term ecological and evolutionary changes in climate-change refugia? We here focus on relatively rapid changes in refugial capacity due to climate change, but long-term ecological and evolutionary changes can occur and be either maladaptive or beneficial for a species, and we need to manage these. For example, a population in a small, isolated refugium that provides moister conditions than the surrounding landscape may evolve greater drought tolerance (potentially beneficial) and/or evolve self-pollination (potentially maladaptive) if its pollinators are not present in the refugium.

What pathways would allow managers to effectively integrate climate-change refugia into the conservation and restoration of degraded landscapes? In many cases, the cost of designing refugia and restoring habitats to high refugial capacity may exceed that of establishing 'future-proofed' stress-tolerant vegetation, and public perception and mitigation cobenefits will be very important. For example, in Australia, exotic trees with broader leaves may be preferred by the public and city planners over narrow-leaved native eucalypt trees, as they provide greater shading and hence greater cooling.

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Declaration of interests

The authors have no interests to declare.

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