

Climate-change refugia: biodiversity in the slow lane

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Climate-change adaptation focuses on conducting and translating research to minimize the dire impacts of anthropogenic climate change, including threats to biodiversity and human welfare. One adaptation strategy is to focus conservation on climate-change refugia (that is, areas relatively buffered from contemporary climate change over time that enable persistence of valued physical, ecological, and sociocultural resources). In this Special Issue, recent methodological and conceptual advances in refugia science will be highlighted. Advances in this emerging subdiscipline are improving scientific understanding and conservation in the face of climate change by considering scale and ecosystem dynamics, and looking beyond climate exposure to sensitivity and adaptive capacity. We propose considering refugia in the context of a multifaceted, long-term, network-based approach, as temporal and spatial gradients of ecological persistence that can act as “slow lanes” rather than areas of stasis. After years of discussion confined primarily to the scientific literature, researchers and resource managers are now working together to put refugia conservation into practice.

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Anthropogenic climate change is predicted to impose an assortment of dramatic effects on society and ecosystems across the globe, prompting resource managers to look for

In a nutshell:

- Climate-change refugia can serve as a “slow lane”, in that their relative buffering from climate change can protect native species and ecosystems from the negative effects of climate change in the short term, and provide longer-term havens from climate impacts for biodiversity and ecosystem function
- Climate-change refugia can be identified and managed by evaluating ecological complexity, scale, and species traits as well as climate and landscape factors
- Natural resource managers now have theory, guidance, and concrete examples to apply the refugia concept in practice

place-based solutions to minimize associated biodiversity losses. The identification, protection, and management of climate-change refugia – generally defined as areas relatively buffered from contemporary climate change (see WebPanel 1 for a glossary of specialist terms) – has increasingly been proposed as a focus of climate adaptation actions to support the persistence of species, communities, and ecosystems, as well as sociocultural values (Keppel *et al.* 2015; Morelli *et al.* 2016). Since the refugia concept was first explored in a modern climate-change adaptation context (Ashcroft 2010; Dobrowski 2011; Keppel *et al.* 2012), technological and theoretical advances, as well as better recognition of practical applications (Anderson *et al.* 2014; Suggitt *et al.* 2018), have created more nuanced ways to identify and conserve these areas (Keppel *et al.* 2015; Morelli *et al.* 2016).

Here, we explain not only how conservation strategies that focus on climate-change refugia increasingly incorporate ecological complexity, including issues of scale and the spectrum of climate-change vulnerability, but also how to consider objectives for climate-change refugia beyond their original static definition. The papers included in this Special Issue discuss how this burgeoning area of study is focused on improving conservation in the face of climate change. We take an inclusive view of climate-change refugia that recognizes the simultaneous importance of conservation in place (“in situ”) and beyond (“ex situ”) (Figure 1). Conservation of in situ refugia can help ensure some continuation of ecosystem services in the near term and preserve unique biodiversity (Keppel *et al.* 2015). Anticipatory planning for ex situ refugia recognizes, for example, the value of locations outside of a species’ current native range that act as “stepping-stones”, aiding long-term efforts to help species track their climatic niche by means of

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passive or assisted migration. Climate-change refugia could also protect sociocultural and physical resources (Morelli *et al.* 2016), although that is not a focus of this Special Issue.

Given that they buffer species and ecosystems from the effects of climate change, refugia can be considered a “slow lane” for resident biodiversity and ecosystem function, embedded within faster climatic changes occurring in the broader landscape or region (Figure 2). As such, climate-change refugia can help to safeguard constituent species and ecosystems for long periods of time; however, they can also be transient, being only lightly or temporarily decoupled from changes experienced in the surrounding landscape (McLaughlin *et al.* 2017). For example, certain freshwater springs have served as refugia through major eco-climatic changes (eg landscape changed from wetlands to deserts) for millennia, whereas most refugial springs are likely to be relatively transient (Cartwright *et al.* 2020). Although all refugia are temporary for their resident species and ecosystem on a long enough timescale, they can provide buffered areas into which the next species or ecosystem can transition.

From a conservation management perspective, climate-change refugia represent potential opportunities to retain biodiversity and ecosystem function in a rapidly changing environment. Numerous challenges remain in identifying these refugia at multiple scales, and in mobilizing a shift in natural resource priorities to ensure that they receive necessary protection on the ground and over useful time spans. In recent years, climate-change refugia science has progressed on several fronts, with methodological advances that have moved the research beyond a narrow focus mostly limited to local-scale, terrain-based protection from climate exposure.

■ Incorporating ecological complexity

Beyond local

Climate-change refugia exist along spatial and temporal continuums (Figure 3; Keppel and Wardell-Johnson 2015), ranging from regional scales (where macrorefugia can facilitate ecosystem persistence over centuries and even millennia), to landscape and local scales (where microrefugia can maintain particular species and communities for years and decades), to “hyper-local” scales (where refuges can provide temporary shelter for individuals) (Fey *et al.* 2019). In addition, disturbance refugia (WebPanel 1) can delay ecosystem transitions for decades or longer (Krawchuk *et al.* 2020).

For conservation planning purposes, researchers recommend integrating environmental metrics targeting a range of refugia types (Ashcroft 2010) and scales (Carroll *et al.* 2017; Michalak *et al.* 2020). Climate-based (ie coarse-filter, broad-scale) macrorefugia can be identified by locating places with low climate-change exposure (Game *et al.* 2011; Belote *et al.* 2018) or low climate velocity (speed and direction needed to maintain the same climate conditions; Loarie *et al.* 2009; Hamann *et al.* 2015), indicating analogous climatic conditions

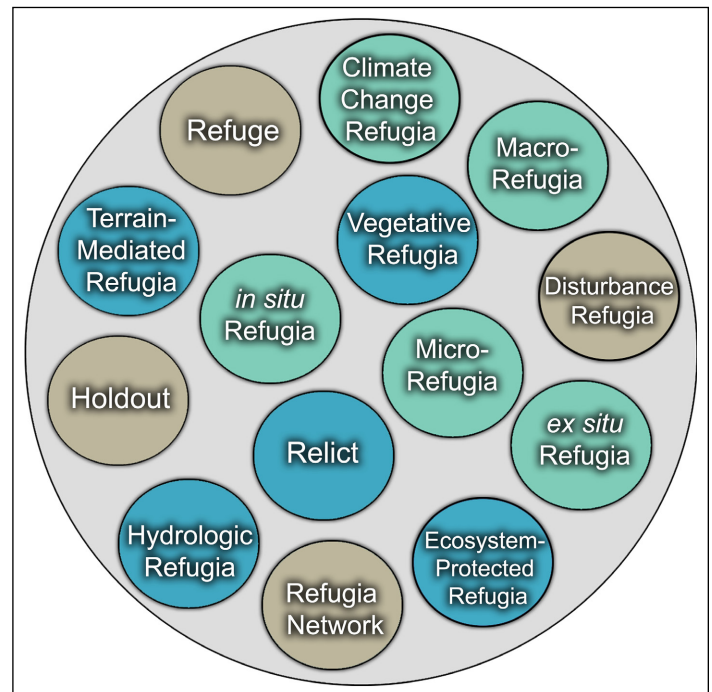


Figure 1. The diverse and expanding terminology of climate refugia, with similar terms grouped by color (see WebPanel 1 for definitions).

either are retained in place or remain in close proximity to their historical locations (Carroll *et al.* 2017). Species distribution models can then identify regions with high species-specific (ie fine-filter) refugia potential (Stralberg *et al.* 2018). Downscaled global climate models project future conditions at a relatively coarse (~1–10 km) resolution (Willis and Bhagwat 2009; Stralberg *et al.* 2018; Michalak *et al.* 2020) and as such might underestimate refugia potential by overlooking microrefugia (Ashcroft 2010; Dobrowski 2011). Incorporating information from a suite of environmental diversity metrics based primarily on relatively fine-resolution (ie 100 m) topographic data can help detect regions with high topographic complexity and therefore high potential for harboring microrefugia (Carroll *et al.* 2017).

In some cases, the areal extent of individual refugia may not be large enough to support subpopulations or populations, but these sites can maintain persistence over time when connected to one another and to protected non-refugial areas (Keeley *et al.* 2018). For instance, highly mobile species such as salmon or migratory butterflies might require networks of small, temporary refuges from exposure. While these might be insufficient on their own in sustaining populations in the face of climate change, such features can play a critical supplemental role in supporting overall climate-change refugia for mobile species (Ebersole *et al.* 2020). Ultimately, combining complementary approaches to identifying refugia that operate at different scales and target different ecological processes will produce a more robust assessment of climate-change refugia potential than relying on a single approach or scale (Michalak *et al.* 2020).

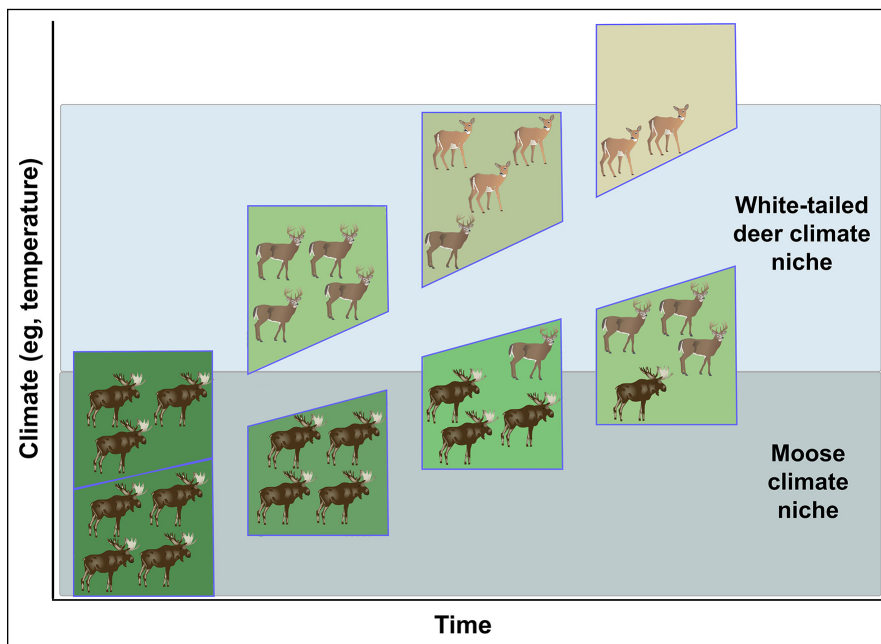


Figure 2. Climate-change refugia create a “slow lane” that enables the long-term persistence of species, communities, and ecosystems despite climate change. As the climate changes over time, both sites (depicted as blue-outlined polygons) ultimately transition from moose (*Alces alces*) to white-tailed deer (*Odocoileus virginianus*) habitat. However, the bottom site transitions more slowly; by allowing resident moose to remain within their climate niche longer, the bottom site serves as a refugium for moose. In the near term, prioritization and protection of refugial locations are key management strategies for selected focal species. In the long term, as climate changes exceed the climatic tolerances of the initial focal species, refugial locations can be managed for transition to other climate-vulnerable species, such as elk (*Cervus canadensis*). Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (www.ian.umces.edu/symbols).

Beyond terrain

Initial descriptions of refugia focused on climatic mechanisms, mediated by terrain. Refugia are therefore traditionally characterized as being decoupled from regional climates and tied to local meteorological phenomena driven by physical terrain characteristics (Ashcroft 2010; Dobrowski 2011; Keppel *et al.* 2012). Many velocity-based macrorefugia metrics heavily emphasize regions with complex terrains (Carroll *et al.* 2017; Michalak *et al.* 2020), although methods have been developed to adjust algorithms to identify topography in relatively flat terrains (Anderson *et al.* 2014). However, other physical and ecological factors beyond terrain contribute to the creation and persistence of refugia (Millar and Westfall 2019; Stralberg *et al.* 2020). Hydrologic microrefugia can be produced not only by topography and soil, which are relatively well-mapped, but also by subsurface hydrogeological structures and processes that are often poorly understood (eg complex groundwater flow paths linking recharge zones to surface discharge as springs; Cartwright *et al.* 2020). In addition, ecological interactions and eco-hydrological processes can confer additional resistance to change in systems like beaver (*Castor* spp)-engineered landscapes, intertidal wetlands, boreal peatlands, and montane uplands dominated by mixtures of rock

and ice known as rock glaciers. Such “ecosystem-protected” refugia – where ecosystem processes provide buffering against climate change – might be particularly important as the magnitude of climate change exceeds the buffering capacity of terrain-mediated refugia (Stralberg *et al.* 2020).

Beyond exposure

Refugia have traditionally been considered as locations that could protect species, communities, and ecosystems from exposure to climate change, primarily focusing on increases in average temperature, but recent studies have evaluated more complex climate stressor gradients, including moisture, snow-pack, stream flow rate and timing, extreme events, and disturbance (Reside *et al.* 2014; Krawchuk *et al.* 2020). “Disturbance refugia” are locations that are disturbed less severely or frequently than the surrounding landscape. In forested ecosystems, the overlap of multiple disturbances can lead to degradation of refugia function in some cases, but resistance to change in others (Krawchuk *et al.* 2020).

In addition to exposure, differences in other aspects of climate-change vulnerability, including how species respond to climate change (sensitivity) and the ability of any individual species to adapt (adaptive capacity), will have a

substantial influence on the location and duration of refugia functionality (Stralberg *et al.* 2018; Michalak *et al.* 2020), as well as the capacity for communities and ecosystems to persist and function. For instance, springs that have flow diminished by climate change but do not desiccate could be refugia for some species (eg plants from the surrounding landscape tracking soil moisture) but not for others (eg obligate aquatic invertebrates) (Cartwright *et al.* 2020). In addition, evidence suggests that species living in landscapes with historically rapid climatic changes have evolved to be less sensitive to those changes (Sandel *et al.* 2011). Bringing these ideas together, Ackerly *et al.* (2020) explore the relationships between regional and local landscape distributions, linking climatic niche and distributions along topographic gradients to species’ projected sensitivity to climate change.

Methodological advances

Considerable advances in modeling and validation have been made over the past decade of research on refugia. Better data, models, and validation (Ashcroft *et al.* 2012; Franklin *et al.* 2013; Anderson *et al.* 2014; Suggitt *et al.* 2018; Ebersole *et al.* 2020; Thorne *et al.* 2020) are improving the spatial

resolution at which climate-change refugia may be identified, as well as the capacity for testing spatial hypotheses on landscape features (Morelli *et al.* 2017; Barrows *et al.* 2020). For example, combining satellite-based mapping or intensive field sampling with climate projections can provide the basis for in situ assessments of climate exposure to identify areas of persistence for vegetation (“vegetative refugia”; Schut *et al.* 2014; Thorne *et al.* 2020) and hydrologic integrity (Cartwright *et al.* 2020) at watershed to ecoregional scales.

■ From management implications to management applications

Resource managers will require innovative strategies to counteract climate-change impacts and better ensure conservation project success, particularly methods that improve communication between themselves, scientists, and decision makers (Enquist *et al.* 2017). Climate-change refugia conservation is poised to shift from planning, which is based on general recommendations, to implementing spatially explicit actions addressing site-specific conditions and network connectivity. Effective management will consider climate-change effects at both large (eg metapopulation, species ranges) and small (eg individual organism) scales that govern adaptive responses to changes in the environment and in management practices (Opdam and Wascher 2004).

In recent years, several tangible examples of refugia conservation practices have emerged (Beller *et al.* 2019). Morelli *et al.* (2016) established the Climate Change Refugia Conservation Cycle (CCRCC), which lays out steps for operationalizing the climate-change refugia management concept. The first steps – identifying management objectives and assessing resource vulnerability – are widely incorporated into climate-change adaptation (Stein *et al.* 2013). The next step, which is unique to climate-change refugia management, involves the mapping and ideally the validation of refugia using physical and biological data. For example, Ebersole *et al.* (2020) describe current efforts by US state and federal agencies to integrate streamflow, water temperature, and interannual patterns of fish distribution to map and evaluate potential climate-change refugia for coldwater fish species. The final steps include selecting and implementing actions to protect the identified refugia, and monitoring outcomes. Successful application of the CCRCC may require (1) modification of prioritization frameworks, (2) evaluation of alternative management actions, (3) a commitment to systematic monitoring, and (4) the capacity to

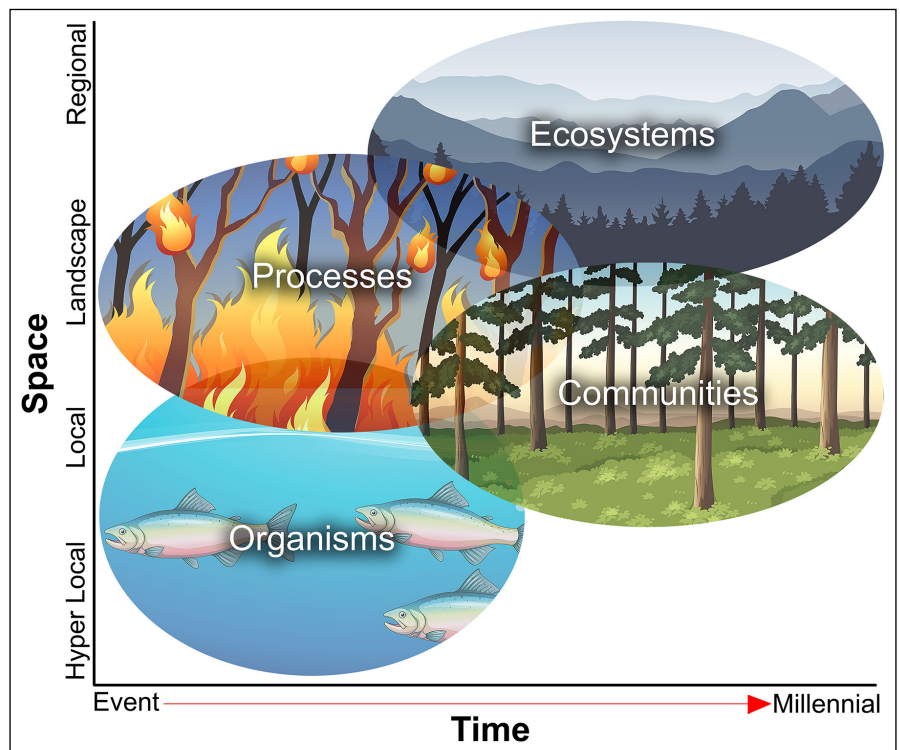


Figure 3. At regional scales, macrorefugia can facilitate ecosystem persistence over centuries and even millennia. At landscape and local scales, microrefugia can maintain selected species and communities for similar lengths of time. At shorter time scales (days to years), hyper-local refuges can provide temporary shelter for individual organisms.

update refugia identification as climate-change projections are refined. For instance, the US Forest Service is incorporating projections of vegetative climate refugia locations into restoration planning for areas affected by the 2014 King Fire in California (Thorne *et al.* 2020). Likewise, The Nature Conservancy has led a proactive planning initiative that focuses on principles of ecological resilience and protection of topographically and geologically diverse landscapes (Anderson *et al.* 2014).

Looking to the future, monitoring of climate-change refugia will become increasingly important for tracking the responses of species, ecosystems, and other resources. Monitoring can be used to detect new threats (Heller and Zavaleta 2009; Reside *et al.* 2018), validate projected change (Morelli *et al.* 2017), and identify threshold conditions beyond which refugia could lose their functionality and become ecological traps, which reduce fitness instead of increasing persistence (Morelli *et al.* 2012). Managers will benefit from systematic, continuous monitoring that spans large spatial scales and time frames of climate and ecological dynamics in areas of particular interest (eg reference sites) and will require dedicated funding. Alternatively, efforts that harness unconventional sources of personnel, such as citizen scientists (eg Barrows *et al.* 2020), may provide additional means of conducting standardized, large-scale monitoring when funding is scarce.

Scales of management

Conceptualizing climate-change refugia as temporal and spatial gradients of ecological persistence – rather than discrete points of stasis (Hobbs *et al.* 2009; Keppel *et al.* 2015) – may improve how resource managers identify and protect them. Different components of biodiversity will respond to climate change at different rates (Hannah *et al.* 2014); monitoring how species shift along climate gradients will reveal their relative risk of local or global extinction (Keppel and Wardell-Johnson 2015). This shift in focus, from stasis to slow change, recognizes the magnitude of anticipated climatic changes, that management intensity may need to increase over time in order to maintain current ecosystem functions, and that changes to management goals may also be necessary. Although adaptive management provides a process for shifting management goals, the time required to complete management activities, from planning to project implementation, might be outpaced by ecological responses on the ground. However, by adopting a climate-change refugia gradient perspective, coupled with an adequate monitoring program, resource managers will be better positioned to anticipate and keep pace with rapid change. Frameworks that enable agencies to collaborate in planning and permitting to address a suite of common ecological responses rather than on a project-by-project basis are especially needed. One way forward is to designate climate-change refugia at local scales (Opdam and Wascher 2004) that exist within landscapes of more general conservation priority (Lawler 2009). For example, the California Department of Fish and Wildlife is using locations of vegetative climate refugia within the range of a suite of vertebrate species to embed climate risk in land management and regulatory considerations (Thorne *et al.* 2020).

Persistence/resistance versus transition/transformation

Climate-change refugia conservation has primarily been invoked as a resistance strategy in the context of climate-change adaptation (Millar *et al.* 2007). Although applicable for resources of particularly high value, we suggest that the scope of management of refugia be expanded. First, unlike natural historical climate cycles, contemporary climate change is probably unidirectional within a societally relevant time frame, barring ambitious political and technological advancements. It is likely that Earth will continue to warm; that precipitation patterns will shift and exhibit escalating extremes at seasonal and annual scales; and that disturbances such as fire, insects, and disease will become even more widespread, frequent, and intense. Therefore, apart from the small fraction of refugia that are fully decoupled, climate-change refugia for most current resident species or other resources are only temporary (Morelli *et al.* 2016; Ackerly *et al.* 2020). Second, managing places to maintain stability at all costs can in some circumstances lead to unintended consequences (Millar and Stephenson 2015), for instance where native

species become increasingly stressed and vulnerable to extensive mortality given an extreme weather event or disturbance. Finally, taking a more broad-scale/network approach could create opportunities for species, ecosystems, and other resources that will soon be the next most vulnerable, as well as those whose distributions are shifting spatially (Figure 2). In this way, conservation strategies could focus on climate-change refugia as places that may be the least affected by climate change into the future (ie the “slow lane”). These places can therefore act as stepping-stones (Hannah *et al.* 2014) to suitable habitats, or as “evolutionary incubators” by allowing time for genetic adaptation to occur, a factor that is of great concern given the rapidity of climate change (Jump and Peñuelas 2005; Hoffmann and Sgrò 2011). This tactic calls for greater focus on slow lane “hold-outs” (Hannah *et al.* 2014) that provide transitional or “relative” refugia value (McLaughlin *et al.* 2017) and help to buy time for species and ecological communities.

We suggest that an effective climate adaptation strategy must encompass targets that are spatially diverse, temporally dynamic, and multifaceted. Climate-change refugia can be managed with a network approach, considering temporary refugia for residents as well as resource transitions and even future refugia for species, communities, and ecosystems previously occurring elsewhere. The result could be novel community assemblages created by the loss of certain species or the gain of others that might lead to ecological replacement, as has happened in the past (Jackson and Overpeck 2000). However, in the context of maintaining ecosystem services in an era of continuous directional change, this dynamic network approach could help achieve conservation objectives (Millar and Stephenson 2015).

Conclusions

As the effects of climate change accelerate, climate-change refugia provide a slow lane to enable persistence of focal resources in the short term, and transitional havens in the long term. Planned wisely, they can serve as stepping-stones for multiple species as climates continue to change. This subdiscipline of climate-change adaptation can generate practical recommendations for resource managers, inform guidance on incorporating ecological complexity at multiple scales considering all aspects of vulnerability, and encourage solutions coproduced by researchers and practitioners. Far from being merely static preserves where species are managed to resist change, climate-change refugia networks can be designed to accommodate changing climates as environments transition to new states.

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