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Conservation strategies for the climate crisis: An update on three decades of biodiversity management recommendations from science

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ABSTRACT

Over the past three decades, climate change adaptation has become a central focus in conservation. To inform these efforts, the scientific community has provided a growing body of recommendations on biodiversity management with climate change. A previously published study reviewed the first wave of such recommendations in the peer-reviewed literature as they occurred between 1985 and 2007. Here we build on that work, reviewing the literature from the subsequent time period, 2007–2017. We report on the development of the field between the two time periods, and review in depth three highly ranked, climate change-specific conservation strategies from the more recent time period. Overall, recommended strategies for ecological management have remained remarkably consistent over the last three decades, and the field continues to draw mainly on conventional, long-standing conservation approaches. However, the actionability and specificity of recommendations have increased, and certain novel, climate change-specific strategies have become more prominent, pointing the way toward increasing options for practitioner response.

1. Introduction

As climate change accelerates, land managers and conservation practitioners must explicitly consider how climate change will affect (or is already affecting) the ecosystems they steward. Scientific guidance is crucial to support this endeavor because it can complement place-based and historical knowledge with new observations, data and modeling. Just over a decade ago, Heller and Zavaleta (2009) published a comprehensive review of scientific recommendations on biodiversity management with climate change. That paper reached both the academic and management sectors and as of this writing has been cited over 1850 times.

At the time of the Heller and Zavaleta (2009) publication, the fields of climate change management and adaptation were in their earlier stages. The paper set a benchmark for the state of the field and highlighted gaps in the literature. It identified the need for more specific and actionable guidance to help managers effectively translate scientific recommendations into on-the-ground practices. It also presented recommendations along a heuristic continuum of risk, and emphasized the value of conservation portfolios that balanced conventional, lower-risk strategies that draw on long-standing practices (e.g., increasing connectivity), with novel, higher-risk strategies that go beyond conventional practices by reorienting toward novel climate futures (e.g., translocating species outside of their known historical ranges). In the time since Heller and Zavaleta's original analysis, projections of climate change and its impacts on biodiversity have become more severe (IPCC,

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2014) and the field of climate change adaptation has developed rapidly. Practical tools, such as downscaled climate models have also become more accessible, and increasingly, federal, state and local agencies, and conservation and land trust organizations are incorporating climate change into management mandates (e.g., Ellenwood et al., 2012; Hagerman, 2016; Harris et al., 2014).

In response to the ongoing frequent citation of Heller and Zavaleta (2009) and the subsequent explosion of new studies in the field, this paper offers an update to the work. Here we ask: what scientific recommendations have emerged to guide the adaptation of biodiversity management to changing climate, and how is that science progressing over time? This work is in the service of helping ecologists and practitioners understand the range and frequency of various climate change adaptation strategies promoted in the scientific literature; anticipating which strategies may increase in practice in the near future; and guiding prioritization and funding of testing and monitoring for frequently recommended strategies to evaluate their effectiveness. We do not independently evaluate the efficacy, value or reasoning behind the recommendations. Finally, we identify broad trends in the literature that showcase research gaps and opportunities.

While other reviews have treated various aspects of the field of climate change adaptation (e.g., Reside et al., 2018; Prober et al., 2012; Hagerman and Pelai 2018; Hagerman and Satterfield 2014; Felton, 2009; Mawdsley, 2009), none have evaluated trends over time in recommendations across the range of taxonomy and analyses we present. Our paper explores whether and how recommendations have changed in geographic scope, ecosystem type, knowledge basis; and, for ecological recommendations, level of actionability and reliance on approaches that are conventional (i.e., those that rely on long-standing conservation tools or strategies) versus novel and climate change-specific (i.e., those that go beyond standard practice and specifically address a changing climate). We compare the relative rankings of ecological recommendation categories, and review in depth the later time period's three most highly ranked novel, climate change-specific strategies that showed substantial increase in relative frequency over time. Given the crisis-level projections of climate change and the growing need to integrate climate change with conservation planning, we expected recommendations to have increased over time in specificity, actionability and geographic scope, and to have shifted toward more novel, climate change-specific approaches.

2. Methods

2.1. Paper selection

The Heller and Zavaleta (2009) data spanned January 1985–March 2007. The recent data set spanned April 2007–December 2017. Papers for both were sourced through a Web of Science (WOS) keyword search in the English language. Because of the prohibitively large number of returns from the original search terms during the more recent time period, the recent set of papers was identified through a focused subset of the Heller and Zavaleta (2009) WOS search criteria, (TS = (climate change OR global warming) and (adaptation OR conservation OR management)), excluding categories irrelevant to biodiversity management (see SI Section S1 for full WOS search criteria for both data sets). The search for the more recent time period returned 9185 papers total. We reviewed a subset of ~10% of these returned papers with apparently relevant titles, stratified by 80 papers per year to ensure that all years within the designated time period were represented. Because the number of papers per year returned from the WOS search increased dramatically between 2007 and 2017 (SI Fig. S1), individual papers in the second data set were weighted by the total number of papers returned in the year of publication. Results using weighted and unweighted values were similar, and weighted results are presented.

Inclusion criteria for papers and recommendations, common to both data sets, were as follows: papers were included if they had a specific recommendation for biodiversity management with climate change. A statement was considered a recommendation if the author suggested a practice, tool or strategy that addressed biodiversity management, conservation or restoration in relation to climate change. We included a statement as a recommendation even in cases where authors presented qualifying statements of risks, challenges or alternatives. A recommendation was included if it contained the key concepts associated with our recommendation categories even if it did not use our specific terms. Papers were excluded if their recommendations focused on management of agricultural species (unless that management directly impacted wild biodiversity), understanding effects of climate change but not *managing* for those effects, the social impacts of climate change (e.g., flooding in coastal cities), or global change but not explicitly climate change. Studies that were only exploratory and did not make specific recommendations were not included in our analyses. Our final analyses included 108 papers from the original data set; and 224 papers in the more recent data, with an average of 21 papers per year. In the recent data set we removed three very large review papers that summarized the field (Mawdsley et al. 2009; Hansen, 2010; Felton, 2009) so that they would not overwhelm the remainder of the data, but kept all other smaller review papers. All review papers were kept in the original data set because of the relatively small number of recommendations covered by review papers at that time.

2.2. Data analysis

For each paper that met inclusion criteria, we extracted data on a suite of variables, described below, and extracted the verbatim recommendation(s) on biodiversity management with climate change. Variable coding was calibrated with the 2009 paper's authors to ensure consistency in category definitions. To increase comparability between the early and recent data sets, all variables in both data sets were aggregated to the paper-level for analysis. Because of this, data presentation in this paper differs from Heller and Zavaleta (2009) in that the data are presented as percentages of papers rather than as percentages of total recommendations. We conducted various analyses on subsets of the data as detailed below (summarized in SI Table S1).

Verbatim recommendations (total = 1069) were coded as ecological management (‘ecological’), social or policy-oriented interventions (‘social’), or call for further study (‘study’), with all recommendations together termed the ‘full data set.’ In the 2007–2017 full data set, the proportion of ecological recommendations was slightly higher than in the earlier data set, with a commensurate decrease in the social and study type categories (SI Fig. S2). Using the full data sets, we compared the geography, ecosystem type, and basis of recommendation between the two time periods. The variable ‘basis’ represented the type of information underlying the recommendation. This information frequently was related to the recommendation but did not specifically test the recommended strategy (e.g. an empirical study on a species' survival rates could have led to a recommendation for assisted migration, but not tested the assisted migration strategy itself). Analyses of climate change metrics, drivers of climate change impact and time scales associated with the climate variable for the recommendations in the second time period are included in SI Section S3.

We further analyzed the subset of individual verbatim recommendations on ecological management (termed ‘ecological recommendations’) from both the original ($n = 305$) and recent ($n = 388$) data sets. We developed a set of recommendation categories (see SI Table S2 for expanded recommendation category definitions) derived from the categories used in Heller and Zavaleta (2009) and the recent data set's verbatim recommendations. Recommendation categories varied in their scope from highly general, such as ‘increase connectivity’ to very specific, such as ‘build shade structure.’ If a statement met the definitions of two categories which were subsets of each other – e.g., ‘manage invasive species’ could be a form of ‘protect ecosystem structure or function’ – the more specific category, in this case ‘manage invasive species,’ was coded. If the statement included two independent categories then both were included (e.g., a recommendation to plant trees to create microrefugia would have been coded as both 'manage for climate change refugia' and 'plant vegetation'). To ensure consistency across the data sets, we re-coded recommendations from the original data set using the new set of recommendation categories. The number of categories into which verbatim recommendations fell were similar between the data sets, with 72 in the earlier, and 73 in the later data set.

For the ecological recommendations, each verbatim recommendation was coded as actionable versus general principle. Actionable recommendations provided a clear directive about what should be done, allowing for implementation in a specific ecological context, while general principle recommendations provided a guiding concept, but were generic, open-ended, and without a clear, implementable directive. Each recommendation category was coded as conventional versus novel, climate change-specific. Conventional recommendations included tools, strategies or approaches that have been used traditionally in ecological management or conservation practice to address threats other than climate change (e.g., 'increase connectivity,' 'manage invasive species'), while novel, climate change-specific recommendations were not used

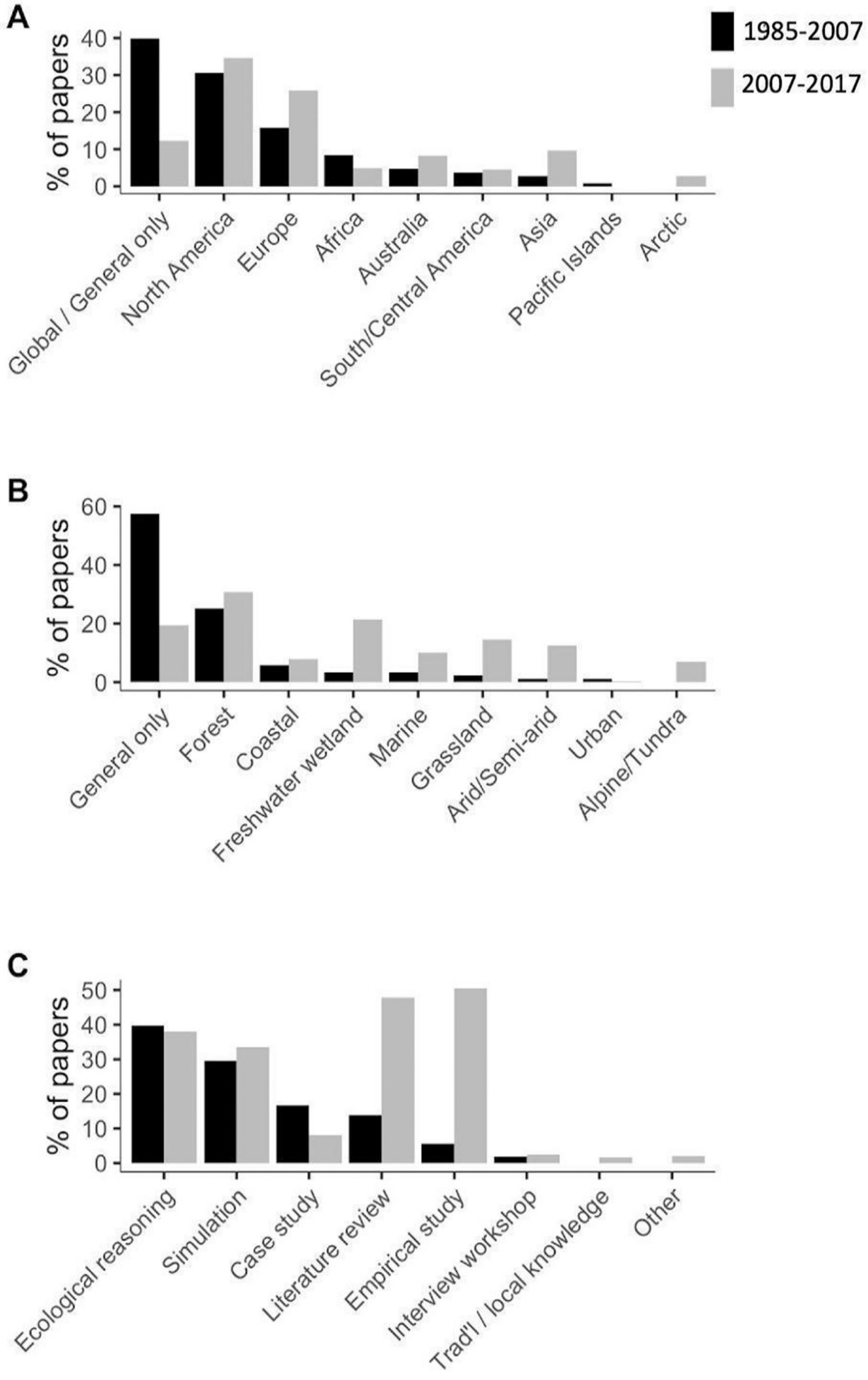

Fig. 1. (A) Global distribution, (B) ecosystem type, and (C) basis for recommendation for the original data set (1985–2007), shown in black, and the recent data set (2007–2017) shown in gray, for the full data set. Values on the y axis may add to >100% because papers could include multiple categories.

Table 1

Ecological recommendations for biodiversity management with climate change in 1985–2007 and 2007–2017. For the top ten recommendations (shaded), red indicates presence in both time periods. Bold-face, italicized type indicates a novel, climate change-specific strategy. Percentage values represent percent of all papers that included a recommendation in the given category. Two additional recommendations are included in both time periods' top ten rankings because of last place rank order ties. Because a paper may have made multiple recommendations falling into different categories, values add to >100%.

Original Data Set (1985-2007)	**%**	**Recent Data Set (2007-2017)**	**%**
Increase connectivity	38	Protect or restore ecosystem structure or function	32
Protect or restore ecosystem structure or function	22	Increase connectivity	20
Manage the matrix	22	***Manage for climate change refugia***	18
Manage at larger scale, or across scales	17	Mitigate non-climatic threats	17
Manage for flexibility/uncertainty	17	Conduct monitoring	13
Conduct monitoring	16	***Climate-adaptive assisted migration (species and populations)***	12
Adaptive management	13	Manage at larger scale, or across scales	11
Species reintroductions within known range	12	Manage for genetic/phenotypic diversity	10
Protect geophysical heterogeneity	11	Forest management	9
Manage invasive species Manage for genetic/phenotypic diversity Mitigate non-climatic threats		***Manage for climate-adaptive genetics*** Adaptive management ***Target future conditions through habitat protection or restoration***	8
Strengthen existing protected areas	9	Manage for community/ecosystem diversity	7
Increase protected area size	9	***Manage for future-adapted species***	6
Manage for climate change refugia	9	Manage fire (suppression or controlled burn)	6
Target future conditions through habitat protection or restoration	8	Protect key biotic features	6
Manage for community/ecosystem diversity	8	Manage for species diversity	6
Manage for future-adapted species	8	Manage the matrix	6
Create or manage buffer zones around protected areas	8	Manage surface hydrology	5
Climate-adaptive assisted migration (species and populations)	7	***Manage climate change threats in combination with other threats***	5
Manage grazing	7	Plant vegetation	5
Build structural or functional redundancy	7	Reduce pollution (air/water quality)	5
Use predictive bio-climate models	7	Captive breeding at botanic gardens/zoos	5
Adopt a long-term perspective	7	Riparian management	5
Manage for species diversity	7	Manage for flexibility/uncertainty	4
Prioritize vulnerable/rare taxa or ecosystems for conservation	5	Natural resource management	4
Irrigate	4	Increase number of protected areas	4
Protect environmental or climatic gradients	5	***Manage for plants that increase mesic microenvironments***	4
Mange fire (burn or suppress)	4	Manage individual taxa	4
Manage surface hydrology	4	Manage invasive species	4
Manage climate change in combination with other threats	4	Manage for structural or functional diversity	4
Manage individual taxa	4	Time/sequence management actions in relation to climate change	4
Address negative impacts of climate change mitigation activities	4	Species reintroductions within known range	4
Restore natural abiotic conditions or processes	4	***Address negative impacts of climate change mitigation activities***	3

Ground management goals in historical conditions	4	***Protect geophysical heterogeneity***	3
Increase the number of protected areas	4	***Protect environmental or climatic gradients***	3
Create longitudinal reserves	4	Manage grazing	<3
Build management goals around ecosystem function rather than species	4	Build structural or functional redundancy	<3
Forest management	<3	Ground management goals in historical conditions	<3
Protect key biotic features	<3	***Connectivity to future habitat***	<3
Connectivity to future habitat	<3	Restore natural abiotic conditions or processes	<3
Riparian management	<3	***Use predictive bio-climate models***	<3
Manage for plants that increase mesic microenvironments	<3	Strengthen existing protected areas	<3
Manage for structural or functional diversity	<3	Prioritize vulnerable/rare taxa or ecosystem for conservation	<3
Protect a species’ leading edge	<3	Consider evolutionary processes	<3
Use caution or don’t use predictive bio-climate models	<3	***Protect a species’ leading edge***	<3
Protect a species’ trailing edge	<3	Irrigate	<3
Manage at community scale	<3	***Prioritize common/non-vulnerable taxa or ecosystems for conservation***	<3
Combine historical and future-adapted species for restoration	<3	Prioritize climate change solutions that have other conservation benefits	<3
Manage soil fertility	<3	Manage individual populations	<3
Manage for climate-adaptive genetics	<3	***Shift goals from historical conditions to current or future conditions***	<3
Plant vegetation	<3	Protect replicate or meta-populations	<3
Reduce pollution (air/water quality)	<3	Adopt a long-term perspective	<3
Captive breeding at botanic gardens/zoos	<3	***Create longitudinal reserves***	<3
Natural resource management	<3	Use indicator species	<3
Shift goals from historical conditions to current or future conditions	<3	Protect groundwater	<3
Protect replicate or meta-populations	<3	***Use caution or don’t use predictive bio-climate models***	<3
Use indicator species	<3	Manage human/wildlife conflict	<3
Manage human/wildlife conflict	<3	Propagate plants	<3
Triage	<3	***Protect a species’ trailing edge***	<3
Reduce pests or pathogens	<3	Triage	<3
Protect networks of reserves	<3	Reduce pests or pathogens	<3
Use caution or do not use indicator species	<3	Protect networks of reserves	<3
Build shade structure	<3	Decrease connectivity	<3
Plan for complex, not just directional changes	<3	Increase protected area size	<3
Protect areas of high endemism	<3	Manage at community scale	<3
Locate protected areas in core of species' ranges	<3	***Experiment with novel approaches in less in-tact landscapes***	<3
Locate protected areas to center on vegetation transitions	<3	***Manage for species with plasticity to adapt to future conditions***	<3
Ecosystem engineering	<3	Use caution or do not use indicator species	<3
Shift goals away from concept of natural	<3	Keep species in current range	<3
Reduce temporal fluctuations in population size	<3	Build management goals around ecosystem function rather than species	<3
Use simple decision-making rules for protected area planning	<3	Create or manage buffer zones around protected areas	<3
		Increase conservation/monitoring in years with extreme climates	<3

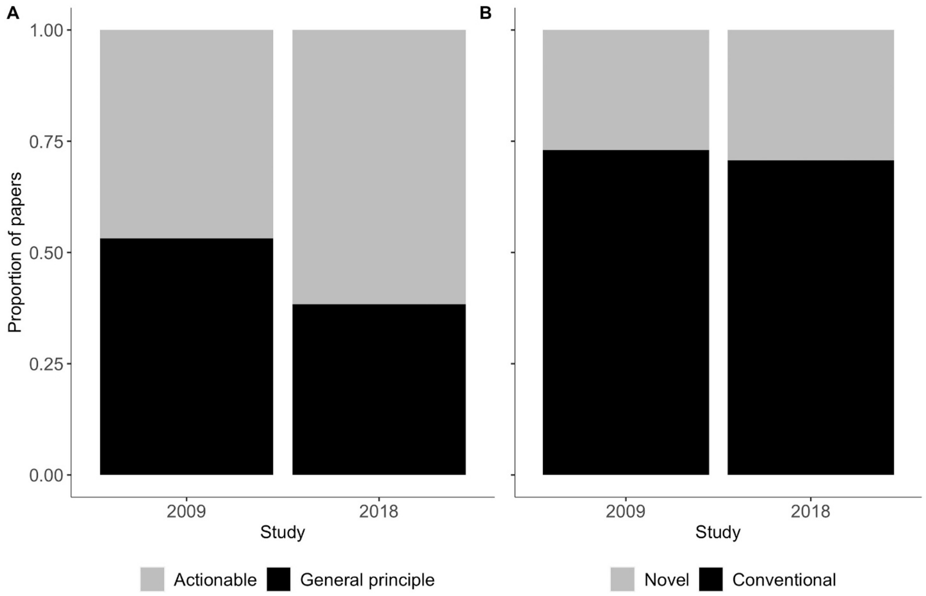

Fig. 2. Proportion of papers with (A) actionable or general principle recommendations, and (B) novel, climate-change specific or conventional recommendations, in the original data set (1985–2007) and the recent data set (2007–2017) (ecological recommendations).

traditionally, and were specifically oriented around a changing climate (e.g., 'manage for climate change refugia'). Finally, we conducted a review of all papers relating to three high-ranking novel, climate change-specific strategies in the more recent time period that increased in relative frequency between the time periods: 'manage for climate change refugia' (original data set $N = 7$, recent data set $N = 31$), 'climate-adaptive assisted migration' (original data set, $N = 4$, recent data set $N = 29$) and 'manage for climate-adaptive genetics' (original data set $N = 1$, recent data set $N = 12$).

Limitations on the analyses in this paper include a lack of perfect comparability between the two data sets. The original data set included all returned papers from the original WOS search, which was possible because of the relatively small number of papers on the subject at that time. In contrast, the more recent data set included a sample of a much larger set of returned papers. Despite the lack of perfect comparability, the trends we present are likely broadly representative of general patterns in the field. There are certainly many additional recommendations in the literature that our review did not identify. Finally, while we hope that recommendations reflect advances in knowledge, we acknowledge that researchers' personal values may influence how they perceive the risks and utility of climate change adaptation strategies, and therefore which strategies they are likely to recommend. For example, researchers' fundamental ethics around active management versus allowing natural progression of ecosystems may impact how they view more interventionist climate adaptation approaches (Aubin et al., 2011).

3. Results

3.1. Full data set

For all recommendation types, we saw an increase in the specificity of geography and ecosystem types between the two time periods (Fig. 1 A&B). General and non-specific recommendations declined as most other categories increased. The geographic location and ecosystem types associated with recommendations were similar between the data sets, with a persistent bias toward forested ecosystems and North America and Europe. We saw shifts in the basis of recommendations, with empirical work and literature review papers increasing in the second time period (Fig. 1C).

3.2. Ecological recommendations

Table 1 displays recommendation categories for ecological recommendations from both time periods in rank order. The percentages represent the percent of papers that included a recommendation in a given category. See SI Table S2 for all recommendation categories with expanded definition and citations. The categories 'increase connectivity' and 'protect or restore habitat structure and function' were ranked in the top two in both time periods, and together were recommended by over half of all papers in both time periods. Between the two time periods, the novel, climate change-specific category 'manage for climate change refugia' doubled from being recommended in 9% of papers to 18% of papers; 'climate-adaptive assisted migration' increased from 7% to 12%; and 'manage for climate-adaptive genetics' increased from <3% to 8%. The one novel, climate change-specific recommendation ranked in the top ten in the first time period, 'protect geophysical heterogeneity,' dropped between the two time periods from 11% to 3%.

Actionable recommendations increased from just below half in the first time period, to almost two thirds in the second time period (Fig. 2A). Although more novel, climate change-specific recommendations ranked in the top ten in the recent time period, the overall proportion of novel, climate change-specific to conventional recommendations remained nearly the same between the two time periods, with approximately three times as many conventional recommendations as novel, climate-change specific recommendations (Fig. 2B).

3.3. Expanding novel strategies

'Manage for climate change refugia,' 'climate-adaptive assisted migration' and 'manage for climate-adaptive genetics' represented the novel, climate change-specific strategies that advanced most strongly in the recent literature, and we review them further below. Our review focuses on the papers selected for this study; overviews of these topics can be found elsewhere (e.g. Morelli, 2016, Morelli, 2020, Aitkin and Whitlock, 2013, McLachlan, 2007, Hewitt et al., 2011).

3.3.1. Manage for climate change refugia

'Manage for climate change refugia' is defined as protecting or improving areas into which species can retreat or persist in the face of climate change (Keppel et al., 2012). The proportion of papers recommending to manage for climate change refugia doubled between the two time periods, indicating a strong growth in promotion of this strategy. Geographic biases largely persisted between the time periods, with the majority of location-specific recommendations in forest and freshwater environments in North America or Europe, similar to trends in the broader data set. However, recommendations about refugia expanded in scope and specificity over time. Papers in the earlier data set focused mainly on refugia from changes in temperature for terrestrial species, and did not identify specific areas for protection. Papers from the more recent data set provided recommendations on a wider range of refugia types, taxa, life stages and climate change-related stressors, and often identified or modeled specific locations for protection or management. Authors frequently acknowledged that biodiversity preservation in refugia might not be sustainable in the long term, but that these efforts can 'buy time' (e.g., Magness et al., 2011).

Authors' conceptualizations of refugia included regional-scale refugia, site-scale or micro-refugia, and genetic refugia. Regional-scale refugia were identified as (1) regions in which climate is projected to remain suitable for a given species or community for the foreseeable future (Jones et al., 2016; Ellis et al., 2007; Zimbres et al., 2012; Scott et al., 2002); (2) geophysical settings that may enable species survival as climate changes (Beier et al., 2015, Hughes et al., 2012, Hellmann and Pineda-Krch, 2007); and (3) places with relatively high projected climate stability (Ramirez-Villegas et al., 2014), or historical climatic stability (Michalski et al., 2017; Spies et al., 2010; Weber et al., 2014) that have acted as refugia in past periods of climate change, such as the US southern Appalachian Mountains. Site-scale or micro-refugia were identified as places where local landscape components buffer the vulnerability of organisms to climate change, such as areas receiving cold air drainage from ice caves (Noss, 2001) or locations with high groundwater availability (McLaughlin and Zavaleta, 2012). Millar et al. (2007) suggested that locally extreme soil types, which have served as refugia for native biodiversity from invasive species, might also reduce vulnerability to climate change. While in the first time period, refugia was conceptualized only as physiographic, in the second time period, the concept of genetic refugia also emerged (Mcleod et al., 2013). Genetic refugia were identified as areas where populations of foundational species historically have experienced high fluctuations in a climate change-related stressor, and therefore may be relatively well-adapted to future conditions and provide refugial habitat to other species. For example, coral communities that have experienced naturally high fluctuations in pH may be pre-adapted to increasing ocean acidification and thus provide genetic refugia for coral-dependent species (Mcleod et al., 2013).

Two main approaches to refugia conservation were advanced. First, for regional-scale refugia, authors recommended conserving lands where models projected high likelihood of future persistence, sometimes with attention to minimum viable population size (e.g., Jarvis et al., 2008; Li et al., 2016). For microrefugia, authors recommended protecting or manipulating the local driver of the refugial conditions. Efforts to enhance the drivers of microrefugia spanned various contexts, such as lowering groundwater withdrawals to decrease pond desiccation and increase moist habitat for amphibians (van Teeffelen et al., 2015), altering streamflow to maintain lower water temperatures for fish (Hupfeld et al., 2015; Crozier et al., 2008), fostering microtopographic tussock structures to enable behavioral thermoregulation for insects (Radchuk et al., 2013), drain-blocking in peatlands to create mesic habitat for craneflies (Carroll, 2010), or modifying built habitat by creating large, poleward-facing, white-painted nest boxes to create cool refugia for chicks (Catry et al., 2011). Multiple authors recommended planting new or protecting existing plants, such as riparian trees or closed canopy forests, to maintain mesic microenvironments that provide refugia (e.g., Crozier et al., 2008; Hupfeld et al., 2015; Jones et al., 2016; Fullerton et al., 2017).

Reflecting the importance of the broader landscape in the function of refugia, authors often offered geographic contexts for refugia recommendations. Some recommended protecting refugia near species trailing edges (Fox et al., 2014), or in areas where refugial and non-refugial habitat were connected by environmental gradients (Abbott and Le Maitre, 2009). Approximately 20% of papers with refugia recommendations also recommended management at larger spatial scales. More than a third recommended protecting refugia in connection with connectivity to allow movement between patches of refugia or to continuous suitable habitat. These examples reflect a valuable melding of novel, climate-change specific and conventional approaches. Overall, the emerging innovative and increasingly specific recommendations on refugia protection have become more actionable and testable since the original review, with improved promise for their use in conservation.

3.3.2. Climate-adaptive assisted migration

'Climate-adaptive assisted migration' included the practices of assisted gene flow, defined as the intentional movement of organisms or gametes between populations within species' current distributions (Aitkin and Whitlock, 2013), and assisted species migration, defined as the intentional movement of species beyond their historical range limits into areas that have or are projected to become climatically suitable (Peters and Darling, 1985). Recommendations for climate-adaptive assisted migration increased from 7% to 12% of papers in the second time period, yet these recommendations frequently were tempered by recognition of potential challenges.

Assisted species migration: Recommendations for assisted species migration increased between the two time periods from 5% to 8%, and in both periods were more prevalent than recommendations for assisted gene flow. These trends contrast with strong opposition to this strategy by some experts in the field (Hagerman and Satterfield 2014, Ricciardi and Simberloff, 2009, Bucharova, 2017, Webber et al., 2011). Authors in the first time period were more hesitant than authors in the second time period to make unequivocal, direct calls for implementation of assisted species migration (Bartlein et al., 1997; Schwartz et al., 2001; Harris et al., 2006), likely reflecting the novelty of the strategy at that time. Recommendations increased in geographic and taxonomic scope between the two time periods. In the first time period, a large majority focused on plants in forest systems in North America. In the second time period, just over a third related to plants and the remainder included corals, invertebrates, mammals and birds. Consistent with trends in the full data set, the specificity of recommendations increased – concept papers dropped from over half to less than a third, and more papers modeled or mapped specifically where to move species.

Authors expressed near-universal concern about the disruptions that assisted species migration could cause to non-target organisms in recipient ecosystems. Some also voiced concerns about risks to translocated organisms themselves (Adams-Hosking et al., 2011; Thorne et al., 2013). Others pointed out that translocations based on climate projections alone could be complicated by non-climatic drivers that shape species distributions, (Magness et al., 2011; Pfeifer-Meister et al., 2013). Noted social obstacles included the political difficulties of moving valuable ecotourism species away from current locations or across political borders (Thorne et al., 2013), existing conservation policies and paradigms that support maintaining species' in their current ranges (Spies et al., 2010; Hewitt et al., 2011), the lack of guidelines on implementation (Thomas, 2011), and the paucity of geographically specific, empirical research to assess ecological viability (Hewitt et al., 2011; Adams-Hosking et al., 2011).

Because of these concerns, most authors presented assisted species migration as appropriate only for species under exceptionally high threat from climate change, as a form of "extreme conservation" (Hellmann and Pineda-Krch, 2007) that should be weighed against the risks of inaction (Lawler and Olden, 2011). Suggested priority candidate species included narrowly-adapted or endemic species with limited natural migration capacity (Jarvis et al., 2008; Spies et al., 2010; Gray et al., 2011; Thomas, 2011); species in geographically constrained landscapes, such as sedentary animals in low-lying islands (Şekercioĝlu et al., 2012) or alpine plants with limited potential for upward elevation dispersal (Ceriani et al., 2009; Thomas, 2011); species in flat regions with very high climate velocity (Jarvis et al., 2008); species in isolated or fragmented populations for which increasing connectivity is not an option (Jewitt et al., 2015; Magness et al., 2011; Jarvis et al., 2008; Jewitt et al., 2015; Marini et al., 2009; Thomas, 2011); and species with high climate change exposure and low resilience (Magness et al., 2011). To minimize negative impacts on the recipient ecosystem, authors generally agreed that species' transplantations should be established within the same broad biogeographic region as their known distributions. Some stated that close attention should be paid to the existing biological communities at the transplant site (Ceriani et al., 2009), and ideally, recipient locations should be free from local endemics (Thomas, 2011).

Finally, some authors gave direction on how to assess the need for and implement assisted species migration. To identify when to begin translocations, authors recommended monitoring existing threatened or trailing edge populations (Galatowitsch et al., 2009; Thomas, 2011). To mitigate the socially unacceptable nature of cutting vegetation for new plantings in protected areas, Spies et al. (2010) recommended using clearings created by wildfire as an opportunity to introduce and establish new species. Others suggested implementing assisted migration projects over multiple years to increase odds of establishment (Galatowitsch et al., 2009), and employing a flexible management approach to respond to establishment failure or emergent negative impacts on the recipient ecosystem (Hewitt et al., 2011). Gray et al. (2011) recommended the comprehensive approach of combining observational work to identify emergent biological impacts, experimental work to explore the impacts of translocation, and modeling to identify recipient sites for transplanted populations. Looking forward, Adams-Hosking et al. (2011) also emphasized the need to protect projected future suitable habitat, into which assisted species migration eventually might occur.

Assisted gene flow: Assisted gene flow recommendations increased from 1% to 5% between the two time periods, and focused mainly on plants but also included fish and invertebrates.

Authors articulated the following goals for assisted gene flow: (1) to help existing populations adapt to changing climate; (2) to rescue unique genetic lineages threatened by a changing climate, such as mountaintop or trailing edge populations; and (3) as an alternative to natural gene flow, e.g. when limited connectivity was desired to prevent invasive species movement. Authors emphasized that assisted gene flow would be most appropriate for species unlikely to adapt to climate change through natural selection, including those with reproductively isolated populations (Sexton et al., 2014), and sessile (Dawson et al., 2013), or physiographically restricted species (Martin, 2010).

Authors generally recommended assisted gene flow on the premise that locally adapted populations may become increasingly maladapted over time to rapidly changing environments (Guerin et al., 2012). However, they recognized the tension between the traditional conservation aim of preserving locally adapted gene pools and the climate change-related aim of intermixing non-local genes to facilitate adaptation to new conditions. Authors noted the possibilities of outbreeding effects (Wilson et al., 2016), and the disruption of distinct genetic lineages (St Clair and Howe, 2007). To experiment with this new strategy in relatively low-risk ecosystems, some authors recommended conducting assisted gene flow through restoration or revegetation projects on degraded lands (Sexton et al., 2014; Gray et al., 2011). Others recommended the preliminary use of common garden experiments to assess the role that genetic diversity may play in climate change adaptation (Harris et al., 2006; Guerin et al., 2012), or genetic testing to better resolve the drivers of observed differences in phenotypes (Guerin et al., 2012). In contrast, others recommended immediate, direct approaches to assisted gene flow adjacent to or within existing populations (St Clair and Howe, 2007).

Assisted gene flow requires the curation of a population that can thrive in both current and future environments (St Clair and Howe, 2007). Because populations must survive a progressively changing and uncertain climate, some authors recommended translocating seed from a range of source site climates to increase genetic diversity in a recipient population (Sexton et al., 2014; Wilson et al., 2016; Guerin et al., 2012; Galatowitsch et al., 2009). Michalski et al. (2017) recommended translocating seed from locations that served as refugia in previous periods of climate change that are associated with high genetic diversity. Alternatively, Guerin et al. (2012) suggested matching source populations directly to a recipient population's projected future climate. While most authors focused on direct climate-related stressors (e.g., drought or heat tolerance), Bridle et al. (2014) addressed impacts of climate change on invertebrates, mediated through community interactions. To promote future success of a butterfly species, they recommended translocation of butterfly populations adapted to a widespread host plant that was likely to persist with climate change, into recipient populations that were specialized on a narrower-ranged host plant that was likely to decline with climate change.

3.3.3. *Manage for climate-adaptive genetics*

Some authors recommended targeting and managing for climate change-adaptive genetics more generally, without explicit calls for assisted gene flow. These recommendations increased from <3% in the first time period to 8% in the second time period, and the majority focused on woody vegetation. They generally called for (1) the protection of existing populations with likely climate-adaptive genetic resources that could facilitate adaptation to climate change in other parts of the species distribution; or (2) management for higher genetic diversity within a population to increase its adaptive potential to climate change. Populations recommended for protection and monitoring included threatened populations that may have climate change-adaptive traits (Hellmann and Pineda-Krch, 2007; St Clair and Howe, 2007), including genetically unique edge populations, that might otherwise be perceived as lower-value, marginal habitat (Diekmann and Serrão, 2012; Wu et al., 2010a, 2010b; Galatowitsch et al., 2009). To increase a population's capacity to adapt to climate change, authors recommended screening planting stock for identified future climate-adaptive alleles (Li et al., 2014); selecting for climate-adaptive traits from within an existing population (e.g., from local microclimates) for planting (Guerin et al., 2012; Rice and Emery, 2003); maintaining locally high genetic diversity through population connectivity (Li et al., 2014); stand management to favor genetic diversity, such as transitioning from coppicing to high forest systems (Pardos et al., 2017); or planting/restoring with broader seed zones (Galatowitsch et al., 2009) and climate-adaptive genotypes that were available naturally through biotechnology (Zheng et al., 2015; Jump et al., 2017; Sexton et al., 2014; Broadhurst, 2013; Gray et al., 2014). The establishment of ex situ collections and captive breeding programs to conserve climate-adaptive genetic diversity (Gray et al., 2011) or increase climate-adaptive traits was also recommended (Hellmann and Pineda-Krch, 2007; Spies et al., 2010).

4. Discussion

Heller and Zavaleta (2009) identified the need for researchers to provide more specific and actionable recommendations on biodiversity management with climate change, and some progress has been made in this direction. Authors provided recommendations with increasingly specific geographic and ecological information. Recommendations around assisted migration and climate change refugia shifted over time to include more species-specific models, maps, and priority locations. Also in the second time period, the proportion of actionable to general principle ecological recommendations grew. This contrasts with Hagerman and Pelai's (2018) review of climate change-adaptive forest management, in which most recommendations were general rather than actionable. This difference may reflect our analyses' broader geographic scope or focus on more recent papers. Together, our findings illustrate that researchers are providing more guidance on where and how to implement biodiversity management with climate change, and less strictly conceptual guidance.

We saw some changes consistent with the expected progression of a new field. These included a shift from conceptual frameworks to fieldwork, empirical studies and literature reviews, and an expansion of geographic extent, with increased focus on Asia and the Arctic, and on freshwater, grassland, arid, marine, and alpine/tundra systems. Yet persistent biases remained. Reliance on traditional ecological knowledge (TEK) increased slightly in the more recent time period, but this category remained below 5% overall (potentially related to the bias of papers in the English language), and represents a valuable, underconsidered source of information on biodiversity management with climate change (e.g., Vinyeta and Lynn, 2013, Pearce et al., 2015). We also continued to see a dominant focus on forested ecosystems and on North America and Europe, consistent with the geographic biases found by Hagerman and Pelai (2018) and typical in other subfields of ecology (e.g., Trimble and Aarde, 2012). Notable gaps in coverage included the Pacific Islands, Africa, and Central and South America. The modest trend observed here in increasing geographical coverage is a positive sign, yet continued work remains to overcome persistent locational biases, which can limit research's usefulness to managers (Matzek et al., 2015).

4.1. Ecological recommendations

Conservation and management responses to climate change have been categorized according to their goals, as resistant versus resilient, transformative, accepting and/or directing (Lynch et al., 2021, Folke, 2006, Millar et al., 2007, Heller and Zavaleta, 2009, Peterson St-Laurent et al., 2021), adaptive versus transformative (Folke et al. 2010, Hagerman and Pelai 2018), or promoting historical versus novel or wild vs. designed ecosystems (Prober et al., 2012, Kueffer, 2014). Broadly, these categorizations distinguish approaches that embrace novel or changing ecological processes and environments from those that attempt to restore historical or sustain current conditions. This paper's categorization of a recommendation as novel, climate change-specific versus conventional averts the challenge of determining the goal of the recommendation (i.e. knowing the ultimate intent of an author). Instead, our categorization relies on whether the recommendation uses a conventional approach that has been applied in previous contexts, or a new approach oriented around climate change.

We expected that the maturation of the field of climate change adaptation, the availability of projection tools, and the increasingly dire predictions of climate change impacts on biodiversity (IPCC, 2014) would lead to more recommendations for novel, climate change-specific tools and strategies in the second time period. Instead, the overall balance of conventional to novel, climate change-specific recommendations has remained nearly unchanged over the past 30 years (Fig. 2B). Recommendation categories in the later data overlapped substantially with those in the earlier period, indicating that there has been more of a reshuffling of (mostly conventional) ideas rather than a proliferation of categorically new ideas on how to manage biodiversity with climate change. The recommendations to 'increase connectivity' and 'manage for ecosystem structure or function' ranked highest in both time periods – over half of the papers in each time period recommended these longstanding, cornerstone conservation strategies (Table 1). Many other top ten recommendations common to both time periods drew on conventional approaches, including to 'mitigate non-climatic threats,' 'manage at larger or across scales,' 'manage for genetic/phenotypic diversity,' and 'conduct monitoring.' These results were partially consistent with Reside et al.'s (2018) review of conservation planning and actions in response to climate change, which found a frequent mention of connectivity; Skikne et al.'s (2021) finding that most proposed adaptation projects included increasing connectivity and restoring ecosystem structure and function; and Beller et al.'s (2020) general ecosystem management recommendations emerging from historical ecology.

Researchers' enduring focus on conventional approaches may reflect hesitations about ecological risks, or an awareness of practitioner constraints based on entrenched conservation paradigms and policies in protected areas (Heller and Hobbs, 2014). Or, these conventional recommendations may have continued to rank highly because they remain highly valuable and effective in a climate change context. The adherence to conventional strategies is generally consistent with the perspectives of biodiversity experts surveyed by Hagerman and Satterfield (2014), which revealed preferences for conventional management actions rather than more interventionist approaches to managing biodiversity with climate change. Similarly, U.S. federal agency managers reported that their agencies would be most likely to adopt conventional, existing conservation strategies for climate adaptation rather than more novel approaches (Kemp et al., 2015).

We focused on the distinction between recommendations for novel, climate change-specific versus conventional strategies because of the influence that continued promotion of mainly conventional approaches could have on practice. The 'law of the instrument' posits that if all one has is a hammer, then everything looks like a nail. Accordingly, the continued promotion of conventional tools and strategies in the literature may shape the range of conservation options explored by managers. While recommendations might understandably reflect current norms, a valuable role for researchers, in collaboration with practitioners, could be to push the boundaries of tool and strategy development to expand the palette of options for biodiversity management with climate change.

Despite continued reliance on mainly conventional approaches, we did see a modest expansion of recommendation types. For example, new recommendations occurred in the second time period that did not appear in the earlier data set. These included recommendations on groundwater management (e.g., van Teeffelen et al., 2015; Essl et al., 2012); using less intact landscapes (those highly invaded or developed) to experiment with more risky techniques (Prober et al., 2012); choosing plant species with high plasticity to adapt to future climate change for restoration projects (Schuler and Orrock, 2012); and increasing monitoring during extreme events (Todd et al., 2008). Notably, recommendations to focus on protecting less vulnerable/common species were present in the more recent, but not the first, time period, and recommendations for prioritizing vulnerable or rare species decreased between the time periods, potentially indicating a shift in focus from saving rare species to maintaining more common species and ecosystem functions. In this case, literature may be out of step with current practice, as many institutions remain heavily invested in, and in some cases legally obligated to focus on, threatened and endangered species management (Heller and Hobbs, 2014).

Certain novel, climate change-specific strategies also rose into the top ten ranking in the second time period. The increase in recommendations for assisted migration occurred in the context of a broader shift away from polarized debates around this strategy toward more nuanced analyses (e.g. Hällfors et al., 2017, Skikne et al., 2020). Recently, more biodiversity experts view this strategy as justifiable under certain circumstances (with highest confidence for woody plants, terrestrial insects and mammals) (Javeline et al., 2015). Despite a current lack of adoption in most current conservation practice (Aitken and Bemmels 2015, Hewitt et al., 2011), some practitioners and funders see a potential role for the strategy in conservation planning (Ogden and Innes, 2007; Reside et al., 2018; Karasov-Olson et al., 2021). Recent models predict high likelihood of assisted migration success when species are translocated to high quality habitats (Peterson and Bode's, 2021), and these predictions are beginning to be supported by assisted migration experiments (e.g. McLane and Aitken, 2012, Willis et al., 2009, McLaughlin et al., 2021), and assessment of translocations in non-climate change contexts (Skikne et al., 2020). However, researchers and biodiversity experts continue to express concerns about risks of non-target species impacts (Peterson and Bode (2021), particularly as the result of translocations of insects, freshwater invertebrates, small mammals and associated pathogens (Javeline et al., 2015), and fish and crustaceans (Mueller and Hellmann, 2008). Guidance on 'chaperoned' assisted migration (Gewin, 2013) and other precautionary approaches (Butt, 2020) offer options for risk reduction.

The jump in ranking that we observed in recommendations to manage for climate change refugia is consistent with the recent attention that this strategy has garnered, such as a 2020 special issue in Frontiers in Ecology and the Environment dedicated to the topic. Projecting climate change refugia also appears to have high uptake with practitioners based on its frequent inclusion in climate-adaptive conservation proposals, planning and actions (Reside et al., 2018; Skikne et al., 2021). The proliferation of refugia recommendations might reflect that its operationalization depends on standard tools, such as land or water protection, and it does not conflict with traditional conservation paradigms or policies. While alignment with traditional conservation norms could explain the strategy's appeal and more immediate uptake, the ephemeral nature of most refugia may limit their long-term effectiveness under continuing, rapid climate change (Reside et al., 2019; Stralberg et al., 2020; McLaughlin et al., 2017).

Only one novel, climate change-specific recommendation from the earlier period's top ten, 'protect geophysical heterogeneity,' dropped down in rankings in the more recent time period. This "coarse filter" approach focuses on conserving geophysical diversity, which might correlate with species and genetic diversity (Anderson and Ferree, 2010) and with diverse microclimates that buffer against extirpations and phenological mismatches (Suggitt et al., 2018; Olliff-Yang and Ackerly, 2020). The decrease in recommendations for this strategy is surprising given its recent adoption by some large conservation organizations. For example, it forms the basis for The Nature Conservancy's national approach to landscape prioritization under climate change (Anderson et al., 2016). However, our results align with other findings that this strategy was included in only 5% of recent climate change adaptation funding proposals (Skikne et al., 2021), and might not be a priority for a broader range of practitioners.

5. Conclusions

Over the last three decades, recommendations for biodiversity conservation with climate change have moved toward greater empiricism, geographic and ecologic specificity, and actionability. Still, many recommendations remain too vague to apply to a specific management context, and are geographically biased toward North America and Europe and forested ecosystems. A clear, enduring reliance on conventional conservation approaches persists. However, our analysis shows some movement toward actualizing proactive, anticipatory, climate change-specific practices. Recommendations for climate-adaptive assisted migration, managing for climate change refugia and managing for climate-adaptive genetics are increasing in number, specificity and actionability. Evidence on the effectiveness of such novel, climate change-specific strategies remains scarce (Conservation Evidence 2021), and the extent to which they already are being recommended in the literature indicates a critical need for increased testing and monitoring. This could be facilitated by researcher-practitioner partnerships, translational approaches (Enquist et al., 2017) and collaborations with holders of local or traditional ecological knowledge (Mistry and Berardi, 2016, Kimmerer and Lake, 2001).

The precautionary principle holds immense value in promoting restraint and preventing unintended harms, and well-tested conservation approaches continue to ground biodiversity management. However, traditional strategies can come with risks of declining effectiveness, lost opportunity costs and unintended consequences that must be weighed against the risks of more novel approaches. The magnitude of the accelerating climate crisis requires aggressive development and testing of innovations in biodiversity conservation for unprecedented climate futures.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

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