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INVITED OPINION

Sustaining Species of the Future: Climatic Nuclei for Climate Change Adaptation

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ABSTRACT

Conservation of climatic refugia, or locations that will buffer vulnerable species from the effects of climate change, has recently emerged as a prominent climate adaptation strategy. Here, we introduce an important and complementary concept, 'climatic nuclei'—locations that harbor populations of species that are expected to expand under future conditions—which has so far received little attention. While the climatic refugia concept focuses on threatened species, the climatic nuclei concept focuses on species that are projected to expand with climate change to help create the functional, diverse, and locally unique ecosystems of the future. We evaluate where climatic nuclei are expected to occur; draw on lessons from the paleoecological and modern ecological literature to better understand how climatic nuclei could function; explore the concept's application to land stewardship and conservation; and provide suggestions for future research.

1 | Introduction

In this century, land and water stewards will navigate climatic changes that have no precedent in modern history in terms of rate and magnitude (Jackson and Overpeck 2000). Species' distributions are shifting; in the future, protected and stewarded areas may no longer support populations of species they were created to conserve (Hobbs et al. 2018). For example, by 2100 the area within Joshua Tree National Park is projected to become largely unsuitable for its iconic namesake tree (Sweet et al. 2019). The expected changes will be devastating, and they are fundamentally shifting conservation needs and practices. Stewards need a portfolio of traditional and novel approaches (Stein et al. 2024) to minimize ecological losses and enable transitions toward desirable and sustainable new ecosystems. Conventional conservation paradigms that rely only on fixed relationships between places and the species that historically occupied those places will no longer suffice, as currently dominant species decline and others expand.

Ecological climate adaptation seeks to address these complex changes and conservation challenges. This emerging field has largely focused on developing management strategies to protect populations threatened with decline, for example conservation of climate change refugia–locations that will buffer vulnerable species populations, at least temporarily, from effects of climate change (e.g., Morelli et al. 2016, but see Gibson et al. 2009). In contrast, largely overlooked in climate-change conservation are the existing populations of native species likely to thrive and expand under future conditions. Many of these species have high ecological and/or cultural value, and may be foundational to the composition and function of future ecosystems. In this paper,

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we introduce the concept of 'climatic nuclei', complementary to climatic refugia and defined as locations that harbor populations that will benefit from and spread in a changing climate.

Consideration of climatic nuclei can help address a broader spectrum of challenges, opportunities, and questions that land stewards are facing. For example: What species in a given landscape will respond positively to climate change? Will a landscape support ecological communities that warrant protected status in the future? If so, what species would comprise those communities, and where might they come from? Climatic nuclei are locations where species that will thrive in the future under climate change now reside. Identifying and protecting climatic nuclei promotes the availability of propagules to populate emerging communities across the landscape under climate change. More interventionist climate-adaptation strategies, such as moving species beyond their known historical distributions, require difficult decisions under high uncertainty. In contrast, protecting native species' climatic nuclei enhances the capacity of species and populations to respond to a dynamic environment (Dawson et al. 2011), potentially creating new and adaptive ecological communities through natural processes.

We adopt the term 'climatic nuclei,' centering on relevance to climate adaptation, and using 'nuclei' to connote the population's potential for expansion, as in 'the action of a nucleus in starting a process' (Merriam-Webster.com Medical Dictionary 2024). This aligns with Yarranton and Morrison's (1974) use of 'nuclei' to describe early-successional species' initial cluster development and expansion. While the concept of climatic nuclei can be applied to a wide range of taxa and ecosystems, here we focus on terrestrial plants because of their foundational ecological and cultural importance. We emphasize heat- and drought-adaptive climatic nuclei, given observed and projected trends in warming and accompanying moisture deficit in many parts of the world (IPCC 2023). Other aspects of climate change (e.g., sea-level rise, fire frequency and severity, flooding) may create different types of nuclei. Unless otherwise specified, we refer to species' climatic rather than geographic distributions. Geographically, the cool edge typically corresponds to the poleward or upper-elevation range margins. However regional climate gradients combined with topographic heterogeneity can decouple the relationships between geographic and climatic distributional edges (Oldfather et al. 2020). As such, climatic distributional edges may occur in many disjunct locations. The scale of climatic nuclei could range from highly local to regional, and would depend on the focal landscape and population.

In this paper, we describe climatic nuclei and where they may occur, and we argue that prioritizing and identifying potential climatic nuclei will be an important addition to a suite of climate-forward conservation strategies. While we mainly focus on species-level climatic nuclei, we also describe the potential for genotypic and ecosystem-level nuclei. To understand how climatic nuclei might function, we draw from paleoecological case-studies of species distributional shifts under past climate change, and from modern ecology, including the roles of 'applied nucleation' in restoration ecology (de Oliveira Bahia et al. 2023; Holl et al. 2024), and of 'nascent foci' in range expansion of invasive species (Moody and Mack 1988). We discuss the relevance of climatic nuclei to various land stewardship and conservation scenarios, and conclude with recommendations for future research.

Conservation and restoration are value-laden fields (Soulé 1985; Baumgaertner and Holthuijzen 2017; Davis and Slobodkin 2004). Climate change inevitably complicates relationships around species and place. Here, we take the perspective that in each place, native species are of value and that as climate change progresses, regionally native species are of higher value than invasive species or species from other biogeographic regions. In practice, stewards and stewardship communities will need to articulate and pursue their own values around focal nuclei species and climate-adaptive conservation.

1.1 | What Are Climatic Nuclei?

Paleoecologists have long observed that local populations on unusually warm, cool, wet, or dry habitats (e.g., pole- or equator-facing aspects, coarse or mesic soils, coastal or continental orientations) can expand to other habitats over broader areas during periods of climatic change (e.g., Blytt 1876). Rather than a continuously advancing peripheral range edge or 'wave front' shifting latitudinally or elevationally with climate change (as is often conveyed in visualizations of climate-induced range shifts), species often advance locally from climatic nuclei—populations in microenvironments at the leading edge or outlier populations that occur beyond the leading edge of the core distribution ("outlier nuclei") (Figure 1). As some local climates

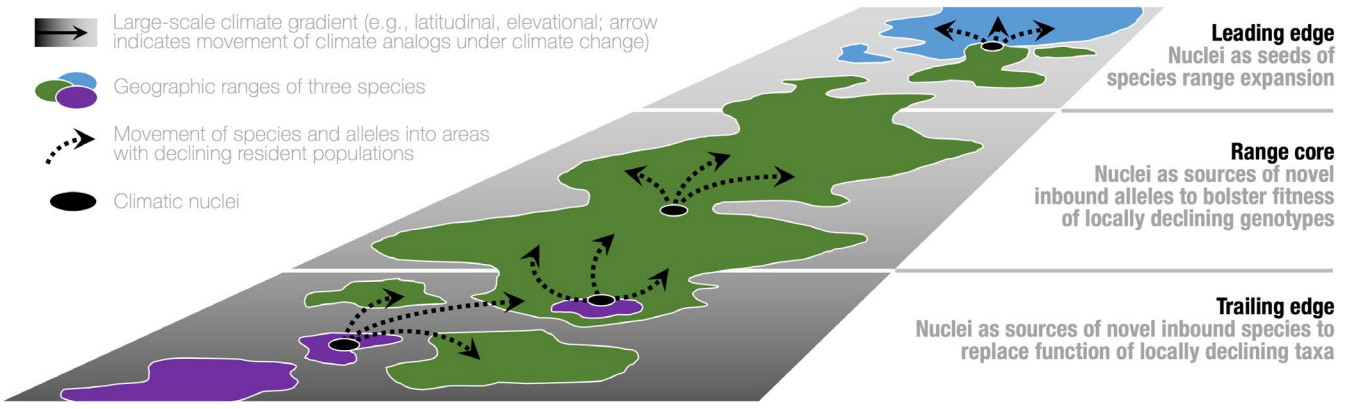

FIGURE 1 | Conceptual drawing of climatic nuclei.

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within a region expand around climate nuclei and others shrink to climate refugia or ultimately disappear, species will track those changes. While in many ways climatic nuclei and refugia could be conceptualized as antiparallel concepts, there are also important differences. Given current climate trajectories, refugia are in essence a 'last stop'; there is nowhere locally for species to go beyond refugia. In contrast, nuclei act as a starting point for range expansion. As expansion occurs, the original nuclei at some point will become embedded within the main distribution, and so will no longer be nuclei. Then, populations at the new expanding edge will become nuclei.

We posit that the location of climatic nuclei will depend on the intersection of three factors (Figure 2). The first is the distribution and dynamics of local climate and environmental conditions that influence moisture and temperature, 'climatic environments.' Climatic environments that are initially rare and are expanding will provide opportunities for species adapted to those conditions to expand in parallel. Second, climatic nuclei will depend on the ecological and physiological constraints of focal populations. Environments may function differently for different species or life stages, sensitive to varying aspects of temperature or water availability. For example, Saguaro cacti (*Carnegiea gigantea*) are particularly sensitive to cold-air drainage and aspect relative to winter sunlight because of their low tolerance for extended subfreezing temperatures (Shreve 1911; Steenbergh and Lowe 1977); many long-lived trees are most climate-sensitive at seedling stages (Grubb 1977; Jackson et al. 2009). Finally, the landscape and biotic context will be important to determine whether locations will serve as nuclei. Landscape connectivity will be important to facilitate species expansion, and the diversity and identity of biotic interactions will influence the likelihood of population establishment and expansion. Major disturbances can play an important role in opening up space for establishment of new populations and disrupting priority effects. Characteristics such as large focal source population size and competitiveness against other resident species, high focal species dispersal capacity and the absence of competitive exotic species, would increase the likelihood of climatic nuclei. By contrast, smaller populations with slow growth and limited dispersal that are surrounded by competitive exotic species might be less likely to function as climatic nuclei.

1.2 | Where Climate Nuclei Might Occur in Local Landscapes

Currently, temperatures are rising globally, and in many areas, warming temperatures cause greater evaporative demand, leading to aridification (even if rainfall is stable or increasing). During a warming trend, climatic nuclei are most likely to be found in sites that are xeric (warm/dry), relative to the surrounding landscape (Table 1). While it may not be immediately intuitive, species occupying such xeric microclimates within

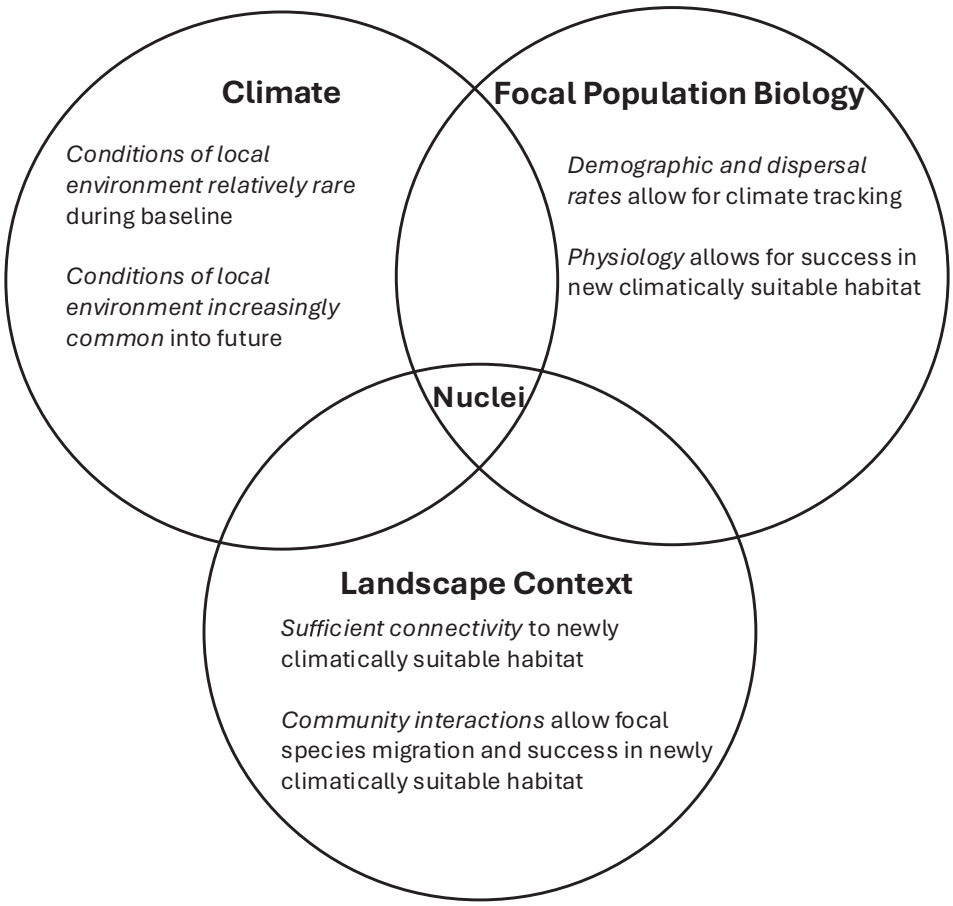

FIGURE 2 | Venn diagram showing the convergence of climate, landscape, and focal population-level factors that influence the suitability of a site as a climatic nucleus.

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a landscape, especially if they are restricted to these microclimates, are likely to be approaching the mesic (cool/wet) edge of their macroclimatic range (Ackerly et al. 2010; Kling et al. 2024).

Warm climatic nuclei could occur in places with low albedo where heat is absorbed (e.g., dark rocks); topographically mediated areas of higher solar radiation (e.g., equator-facing slopes) (Dobrowski 2011; Geiger et al. 1995; Kling et al. 2024; Weiss et al. 1988); or areas with lower tree cover and shading, such as where low soil fertility restricts tree growth. Lower elevations are generally warmer than higher elevations, but cold-air pooling in topographic depressions can create localized temperature inversions that make depressions substantially cooler than surrounding uplands (Samways 1990, Dobrowski 2011; Van de Ven et al. 2007). Microenvironments with higher snow cover (McLaughlin et al. 2017) can insulate plants from freezing winter temperatures (Billings and Mooney 1968) and could support winter-warm nuclei. In regions projected to become warmer and wetter with climate change, surface geothermal areas that can influence the growing temperatures of surrounding plant communities (Stout and AL-NIEMI 2002) could potentially act as climatic nuclei.

Dry climatic nuclei could occur where environmental conditions confer locally low plant water availability, surrounded by an overall more mesic landscape (Table 1). These nuclei could be topographically mediated, including steep slopes, rain-shadowed locations, or wind-exposed topographic positions (Kling et al. 2024). Such local topography can confer substantial microgeographic differences in soil moisture (Kling et al. 2024). Dry nuclei could also occur at the dry ends of subsurface hydrologic gradients that limit subsurface water availability for deep-rooted species (e.g., upland locations on channel/hill gradients (McLaughlin et al. 2022). Places where soil characteristics limit plant water availability, “edaphic nuclei,” could include coarse, sandy, rocky, thin or otherwise highly drained soils with low water-holding capacity (Griffin 1964) such as volcanic outcrops. However, coarse-textured soils can also function to support deeper percolation and water availability for deep-rooted trees and other perennial plants, the ‘inverse texture effect’ (Noy-Meir 1973), which could cause these areas to function as refugia for some species instead of nuclei. Specialized soils such as serpentine (Harrison et al. 2015) have many of the potential characteristics of nuclei. However, results are mixed on the climate vulnerability of species on specialized soils (Damschen et al. 2012), which may be uncompetitive with more generalist plants in surrounding less specialized soils.

There are well-documented examples of populations in such warm or dry environments at or beyond the cool or wet edges of species' core ranges that could form climatic nuclei. These include the extension of treelines into warm microclimates such as equator-facing sites at both high elevations and latitudes (e.g., Danby and Hik 2007; Quadri et al. 2021. Hammocks of tropical hardwoods exist in south Florida in outlier populations beyond their core distributions (Roberts et al. 2017) and may seed the spread of tropical flora northward into continental North America with climate change.

A common California example of potential edaphic nuclei is occurrences of drought-adapted chaparral shrubs on thin soils or serpentine outcrops amidst surrounding coniferous woodlands, even on cooler, pole-facing slopes (personal observation, authors). These areas could act as species-level nuclei if a single dominant species spreads with climate change, or as ecosystem-level nuclei if whole suites of chaparral species expand into the surrounding environment, shifting the overall system from a coniferous forest to a chaparral shrubland. Because chaparral species are generally more fire- and drought-tolerant than forests, these nuclei could act as fire and/or drought nuclei if the surrounding forests were lost to increasing drought or wildfire. The idea of fire-adapted nuclei has a parallel concept in fire refugia (Meddens et al. 2018).

Both modeling and field studies support the idea that illustrate the function of climatic nuclei. In recent modeling work of a topographically variable landscape in Central California, Ackerly et al. (2010) coupled maps of local species' distributions across topographic gradients with projected future species distribution models. Theyfound that species occupying south-facing slopes at their mesic range edge were projected to have stable or increasing suitability under future climates. Field evidence consistent with the contemporary function of species-level climatic nuclei for Utah juniper (*Juniperus osteosperma*) was reported by Lyford et al. (2003), who documented that outlier populations north of the species' main distribution have recently been expanding into previously unoccupied areas of the surrounding landscape with climate change.

1.3 | How Are Climatic Nuclei Formed?

In and out of an ice age: Notably, yesterday's climatic refugia may be tomorrow's climatic nuclei—at varying points of time in Earth's history, a locale might serve alternately as refugium and nucleus, depending on the direction of climate change. Under climate warming, cool microsites may serve as refugia and warm microsites as nuclei, while their roles might switch during climate cooling. In this way, current climatic nuclei may be refugial relicts of past climates (“relictual nuclei”). For example, warm sites that support populations at the cold edge of a species range (i.e., potential nuclei under future warming) may be historic refugia to which the species retreated during past regional cooling. Alternation of sites and populations between refugia and nuclei is documented in biogeographic patterns (Blytt 1876) and paleoecological records. For example, in the warm and dry early Holocene, the central Adirondack Mountains supported substantial populations of *Quercus* (Whitehead and Jackson 1990). Today *Quercus* is restricted to small, isolated refugial populations on equator-facing slopes (Kudish 1992), which could become nuclei for regional (re)expansion under climate change. Other refugial or relict populations from the early Holocene that could become future nuclei include remnants of the eastward extension of prairie in the Midwest (Williams et al. 2009), and outwash-plain populations of *Pinus banksiana* in the northern Great Lakes region that formerly occupied more mesic soils under drier climate (e.g., Brubaker 1975; see also Axelrod 1981).

Alternatively, climatic nuclei could be more recently established through long distance dispersal (“LDD nuclei”) or ongoing ‘wave’ migration. In addition to climatic nuclei that form through natural causes, human-induced environments

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that create low albedo, solar radiation exposure, low soil water holding capacity, or high surface temperatures could also function as "anthropogenic nuclei." Anthropogenic nuclei might include urban heat islands, or areas that have been cleared or logged (causing them to become more arid) where relatively dry-adaptive species have established. Parks and gardens (particularly green roofs that are often relatively warm and dry because of shallow planting substrates and exposed locations) that are planted with warm/dry-adapted species (native or non-native) may function as seed sources for climate-driven expansion into adjacent natural areas.

Without some knowledge of a focal species' environmental and biogeographic history, it could be challenging to disentangle the various source types of climatic nuclei. And, while the knowledge of a population's history could be helpful in assessing how best to support a climatic nucleus—(e.g., the genetic diversity in a relict nucleus may be higher than in an LDD nucleus), for climate-adaptive conservation, all climatic nuclei could be relevant. Therefore, for the purposes of the remainder of this paper, we generally do not distinguish amongst their various source types.

1.4 | Ecosystem Nuclei

Rather than functioning at a species level, climatic nuclei could function at a community level, creating ecosystem nuclei. Ecosystem nuclei could occur where xeric environments support assemblages of future climate—adapted species that thrive and expand with climate change. Communities will likely disaggregate to some extent under climate change (Jackson and Overpeck 2000) both because of individualistic species responses (Rapacciuolo et al. 2014) and future novel climates (Williams et al. 2007). However, an ecosystem nucleus could support multiple foundation or keystone species that move in tandem and promote ecosystem-level shifts across the landscape. Ecosystem nuclei could be particularly relevant for ecosystems dominated by a few foundation or keystone species, and less so for very high-diversity systems with lower potential for aggregate movement. Ecosystem nuclei could occur both at small scales (e.g., where pockets of chaparral exist within a landscape dominated by coniferous forest—see example above) or regional scales (e.g., ecosystems buffered by temperate marine environments that extend in narrow bands along the coast into northern latitudes where inland climates have been unsuitably cold).

1.5 | Genotypic Nuclei

Populations with local adaptations across a range of hydrologic and thermal microenvironments (Epperson 1992, Vekemans and Hardy 2004, Lara-Romero et al. 2016, Sandurska et al. 2024, Ennos 2001, Troupin et al. 2006, reviewed in Denney et al. 2020), could support 'genotypic nuclei' (Figure 3). Genotypic nuclei could provide sources of future climate-adapted genotypes to their broader populations (similar to the ways in which species-level nuclei provide sources of future climate-adapted species to surrounding landscapes). Genotypic nuclei could shift overall population genetics toward more warm or dry-adapted alleles, in a form of evolutionary rescue (Gomulkiewicz and Holt 1995).

Genotypic nuclei could be currently located in populations where seed dispersal across microenvironments is not climatically mediated, but where climatic barriers to recruitment or reproduction create different selection pressures across different microenvironments (e.g., in trees with climate-sensitive early life stages (Grubb 1977, Jackson et al. 2009)) (Figure 3). This could allow proximate subpopulations to maintain genetic differentiation and avoid genetic swamping (Haldane 1956; Kirkpatrick and Barton 1997). The reproductive isolation of a genetic nucleus could be amplified by microclimatic impacts on phenology (Koenig et al. 2015). Emergent and future climate change could then reduce establishment barriers and cause

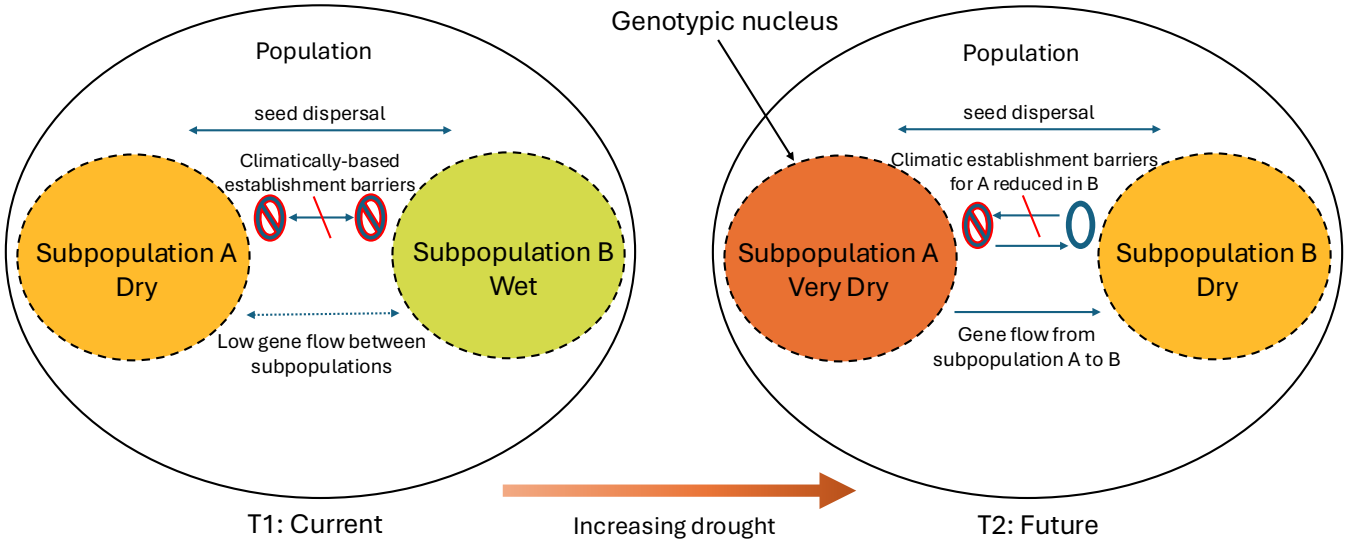

FIGURE 3 | Conceptual diagram of genotypic nuclei, showing the same population at T1, current, and T2, a future drier time period, with subpopulation A in a relatively dry and subpopulation B in a relatively wet microclimate. Subpopulation A functions as the genotypic nuclei, spreading more drought-adaptive alleles into Subpopulation B as climate changes and climatically based barriers to establishment of the dry-adaptive alleles from subpopulation A are reduced. Seed dispersal between subpopulations is not climatically mediated and occurs in both time periods.

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dry-adapted individuals to be favored across the population, allowing a genotypic nucleus to spread (Figure 3). Because of lags in climate-change impacts on adults relative to seedlings (e.g., McLaughlin and Zavaleta 2012), genotypic nuclei could provide climate-adaptive genotypes to the broader population, even as the nuclei's location became too dry for further hyperlocal recruitment.

Certain population or landscape contexts could promote genotypic nuclei. Genotypic nuclei may be more likely to occur in populations with higher overall diversity, such as those in previous regions of glacial refugia (Silvertown and Antonovics 2001), that would allow for selection of micro-geographically adapted subpopulations. Genotypic nuclei also would only occur where a population crosses a range of microenvironments. Because species often constrict to a single favorable microenvironment at their range edges (Ackerly et al. 2010; Kling et al. 2024), genotypic nuclei may be more likely in populations that occur in species' range centers. Populations of plants that only reproduce clonally would be less likely to contain genetic nuclei because of the lower potential for gene flow across contrasting microenvironments. Common garden experiments and rapidly evolving genomics tools could help determine whether subpopulations in contrasting microenvironments are genetically unique, and whether a particular subpopulation contains future climate-adaptive genotypes and likely genotypic nuclei.

2 | Lessons From Paleoecology

Paleoecological studies document the importance of climate nuclei in past local and regional population expansions following climate change and illustrate patterns and mechanisms of nucleus dynamics. In eastern North America and Eurasia, small, isolated populations of several boreal and temperate tree species, far north of their primary ranges during the last glacial maximum, are now well-documented from paleobotanical evidence (Jackson et al. 2000; Magri et al. 2006; Binney et al. 2009). Although their local habitats remain largely unknown, the broader paleoclimatic context and regional vegetation (e.g., tundra-woodland or boreal-dominated forest) suggest that they must have persisted in suitable microhabitats that offset the unfavorable regional climates. Studies of ancient DNA from sediments and fossils, and modern phylogeographic patterns, are providing independent evidence. For example, sedimentary ancient DNA suggests glacial-age occurrence of *Picea* in tundra near the Scandinavian ice sheet in northwestern Norway (Parducci et al. 2012), and Nota et al. (2022) demonstrated haplotype continuity of *Picea abies* from the present to ice-adjacent populations at least 14,700 years BP in southern Sweden. In eastern North America, phylogeographic studies indicate that local populations of cool-temperate tree species (*Acer rubrum, Fagus grandifolia*) grew as far north as the Ohio River valley (McLachlan et al. 2005), in regions dominated by boreal conifers (Liu et al. 2013). In the diverse topography of western North America, many montane and subalpine species occurred on locally suitable microhabitats across much of the region. For example, woodrat-midden evidence indicates glacial-age occurrence and persistence of *Pinus flexilis*, *Pseudotsuga menziesii*, *Pinus pungens*, *Juniperus scopulorum*, and other species on south-facing rocky escarpments at multiple sites in the central Rockies (Betancourt 1990; Jackson et al. 2005). Occurrence of these latter populations is by itself insufficient to verify that they were climate nuclei. However, phylogeographic patterns indicate that many similar populations did indeed serve as sources for upward expansion and northward migration during the late-glacial and Holocene (McLachlan et al. 2005; Magri et al. 2006; Nota et al. 2022).

Although poleward migrations of species during the last deglaciation and through the Holocene are often perceived as steady frontal movements, networks of spatially and temporally precise paleoecological studies indicate that many range expansions were patchy, often paced by climate variations (Davis et al. 1986; Woods and Davis 1989; Payette 1993; Peñalba and Payette 1997; Lyford et al. 2003; Jackson et al. 2009; Payette et al. 2022). The westward migration of *Fagus grandifolia* and *Tsuga canadensis* across Upper Michigan consisted of serial population establishments by long-distance dispersal, followed by expansion and backfilling (Davis et al. 1986; Woods and Davis 1989). Early to mid-Holocene climate in eastern North America and Europe was warm and dry, with cooling and increasing effective moisture in the late Holocene (Marsicek et al. 2018). In eastern North America, prairie expanded eastward in the early Holocene, retreating in the late Holocene (Baker et al. 1996; Williams et al. 2009), and many temperate tree species established populations at higher latitudes and elevations before retreating southward and downward (Terasmae and Anderson 1970; Jackson 1989; Liu 1990; Spear et al. 1994). Remnant high-elevation and high-latitude populations of these tree species, and of prairie species in the central US, may serve as climate nuclei under warming and drying. Although boreal conifers (*Picea* spp., *Abies balsamea*, *Larix laricina*) declined regionally in the Great Lakes/St. Lawrence region in the early Holocene, they persisted in local cold-air drainages and wetlands, expanding from these nuclei in the late Holocene to occupy a broader array of habitats and develop larger regional populations under cooling and wetting (Webb et al. 1983, Jackson et al. 1997).

Spatially precise studies, based on dense sampling of woodrat middens, of Holocene migration patterns of several tree species of western North America show the importance of local habitat and climate variability in nucleus establishment, persistence, and expansion. *Juniperus osteosperma* expanded northward from the Utah/Wyoming border region via serial establishment of nucleus populations through long-distance seed dispersal (Lyford et al. 2003). Populations were established on bedrock exposures in mountain foothills and basin escarpments during warm and dry periods, persisted through intervals of unfavorable climate, and served as nuclei for further expansion—and, importantly, backfilling—during subsequent warm and dry episodes (Lyford et al. 2003; Norris et al. 2016). Within the past century, the species has been expanding again, with expanding nucleus populations as well as dispersal into previously unoccupied canyons and scarps (Lyford et al. 2003). Woodrat-midden data indicate that the northernmost large population of *Pinus edulis*, on a south-facing escarpment on the northern flanks of the Uinta Mountains, was established via long-distance dispersal and subsequent expansion less than 800 years ago (Jackson et al. 2005). Initial establishment occurred during a relatively

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moist period, which was followed by a severe multidecadal drought, and then by a 50-year pluvial of unusually high precipitation (Gray et al. 2006). The founding *P. edulis* individual survived the drought and served as the nucleus for establishment of *P. edulis* over a 2-km span of the escarpment during the initial pluvial. Further expansion during subsequent moist periods led to dominance of the species across an area spanning $>25\,km^2$ (Jackson et al. 2005; Gray et al. 2006).

Pinus ponderosa populations in the western foothills of Wyoming's Bighorn Mountains were established 1500–1000 years ago (Norris et al. 2016) and served as nuclei for 16th and 17th Century long-distance dispersal (15 to >100 km) to four isolated escarpments in the arid Bighorn Basin to the west. Subsequent expansion of those outlier populations was mediated by a combination of climate variability, demographic processes, and Allee effects (Lesser and Jackson 2012, 3013; Lesser et al. 2013). *P. ponderosa* is a poor self-pollinator, so expansion of the isolated founding populations was paced by accretion of genetic diversity through long-distance pollen and seed dispersal (Lesser et al. 2013). These populations may serve as nuclei for establishment of populations in the Absaroka Mountains and Yellowstone Plateau 50–100 km to the W and NW; niche-envelope models suggest suitable habitat emerging in those regions under some climate-change projections (Shafer et al. 2001; Rehfeldt et al. 2006).

3 | Insights From Modern Ecology

Below we discuss particularly relevant perspectives from the fields of restoration ecology, invasion ecology, and population and community ecology. These, as well as many other fields in ecology, can inform our understanding of how climatic nuclei may function with current climate change, and what role they could play in climate-adaptive conservation.

3.1 | Restoration Ecology

'Applied nucleation' in restoration ecology refers to multiple, dispersed small-nucleus restoration plantings intended to spur species' establishment and spread throughout degraded sites (reviewed in de Oliveira Bahia et al. 2023 and Holl et al. 2024). In a range of ecosystems, applied nucleation can facilitate species' restoration without the effort of continuous planting (de Oliveira Bahia et al. 2023; Holl et al. 2024; Procknow et al. 2023). Further, by creating habitat, applied nucleation can be used to support additional biodiversity that would otherwise not be able to immigrate into a landscape (Brooks et al. 2009). While applied nuclei are intentionally established islands of plants in currently degraded landscapes, climatic nuclei are pre-existing and persisting islands of plants within a surrounding landscape that may soon become 'degraded' by the mismatch of future climate to much of the present biota. Conserving climatic nuclei now could proactively support the future "restoration" capacity of the landscape, where eventually, climatic nuclei may function similarly to applied nuclei. Therefore, despite different contexts, lessons from studies of applied nucleation can inform the development of conservation approaches for climatic nuclei.

Applied nucleation research points to the influence of ecosystem type, species' life history, and community interactions on the technique's success (de Oliveira Bahia et al. 2023; Holl et al. 2020, 2021). Focal species in more productive ecosystems, with higher growth, demographic and dispersal rates, and with more competitive recruitment strategies increased the restoration success of applied nucleation. Conversely, the presence of competitive invasive species reduced restoration success. This body of research underscores the importance of considering the ecosystem context, and demography and life history of focal species for climatic nuclei in conservation planning. In low-productivity ecosystems or for focal species that have slow life histories, limited dispersal, inhibited recruitment, or low competitive ability, climatic nuclei conservation strategies may need to be used in conjunction with other management approaches that address negative community interactions and improve habitat suitability. These approaches could include invasive removal, or direct planting of seeds from the nuclei and protection of seedlings, to encourage expansion. Choice of focal species for applied nucleation can also guide choice of focal species for climatic nuclei. Species used in applied nucleation are often foundational and habitat-forming, such as woody shrubs or trees, because of their often large influence on ecosystem structure and function. Certain woody species can initiate successional processes that support additional native species and suppress understory invasives that exclude understory natives (e.g., Corbin and Holl 2012; Holl et al. 2020). Analogously, climatic nuclei for such foundational species may support broader landscape resilience by creating patches of habitat or 'stepping stones' (Hannah et al. 2014) to more continuous habitat for other native species whose ranges also are shifting with climate change.

3.2 | Invasion Ecology

The field of invasion ecology has long utilized the concept of nucleation to explain invasive species spread across the broader landscape from small, outlier populations beyond the core distribution (Moody and Mack 1988). These outlier populations, in invasion ecology referred to as "nascent foci," can serve as important propagule sources for an expanding invasion front, and the establishment of many discreet nascent foci can accelerate an invasion (With 2002). Similarly, as newly suitable habitat opens up at focal species' leading edges, a landscape configuration in which climatic nuclei already exist may accelerate the 'invasion' (in a positive sense) of future climate-adapted species across the landscape.

The drivers underlying invasions frequently include release from enemies and competitors, so invasion dynamics may differ from predominantly climate-induced range expansions. However, lessons from invasive species' expansion can be relevant to the expansion of native or regionally native species with climate change, and help guide how and where to conserve potential climatic nuclei. For example, to effectively control invasions, multiple studies recommend that nascent foci be prioritized for eradication before addressing the main population (e.g., Moody and Mack 1988; Mack and Foster 2004; Gorchov et al. 2014). Conversely, one could prioritize the protection of outlier nuclei to foster native species'

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climate-induced range expansion. Suggested strategies to slow invasive species spread include scouting for and eradicating nascent foci in potentially suitable habitat 4–5 km from a main population (based on estimates of the species dispersal distance) (Gorchov et al. 2014). Conversely, such scouting, based on a focal species' estimated dispersal distance from known leading edge populations, could help to identify and prioritize potential climatic nuclei for protection. In invasive species studies, the absolute number of nascent foci has been proposed as more important than their size (Mack 1985), which could indicate the importance of identifying and protecting as many climatic nuclei as possible.

The importance of nascent foci also depends on whether population expansion is dominated by diffusion or long-distance dispersal and whether the nascent foci are recruiting internally (Shigesada et al. 1995; Gorchov et al. 2014). These dynamics could similarly impact climatic nuclei and inform approaches to protect them. For example, a climatic nucleus created by a park within an urban heat island may hold important future climate-adapted species for surrounding landscapes, but expansion by diffusion may be limited because of habitat fragmentation. If long-distance dispersal is possible for these species, the park may still function as a nucleus; if not, human assistance would be required to facilitate expansion.

3.3 | Population and Community Ecology

Population and community ecology can also inform understanding of how climatic nuclei could function and what factors could mediate or control nucleus-to-'core' transformation. We discuss only a few key points here. Perhaps most importantly, a functional climatic nucleus would require that the focal species' reproductive and dispersal rates keep pace with climate change. In a case of very rapid climate change and a nucleus species with limited dispersal and slow reproduction, the nucleus may become climatically unsuitable before the species has a chance to spread and establish adjacent populations. Once established, seedlings must survive to reproductive age, and newly established populations must be able to persist despite environmental variability and continued climate change, at least long enough to grow and spread further. Dynamics of propagule dispersal, recruitment, and post-establishment persistence at new sites will be important in how quickly nucleus populations can spread. Where climate change outpaces species capacity for movement, more interventionist approaches would likely be needed.

A key principle of the theory of population expansion is that the rate of spread is a function of total fecundity, or propagule flux density, at the leading edge (Clark et al. 1998). Therefore, a population's size (as a fecundity proxy) could influence its likelihood of serving as a climatic nucleus; management for increased population size and total reproductive output in a potential climatic nucleus population could increase its likelihood of expansion. Small nuclei or recently established populations could be vulnerable to genetic bottlenecking and Allee effects, potentially requiring seed or pollen inputs from other populations through long-distance dispersal (e.g., Lesser and Jackson 2013), and/or management to reduce other stressors.

Facilitative, competitive, predatory, and/or pathogenic interactions also will influence a population's potential to act as climatic nuclei. In recipient sites, species must establish, grow and persist in the face of competition from local incumbents, other species moving into the same site, and potentially novel herbivores. As climate shifts, suites of species that typically occur together may not track climate together (Lurgi et al. 2012). Resulting changes in community interactions may limit (or enhance) a species' success in new climatically suitable habitat. For example, for plants with mycorrhizal associates that support an increased range of host climate tolerance (Bahadur et al. 2019), a lack of mycorrhizal dispersal along with seeds into newly climatically suitable habitat could limit spread.

4 | Climatic Nuclei and Land Stewardship

Managing for ecological transitions with climate change, including for climatic nuclei, will necessitate fundamental changes in stewardship approaches, including cross-boundary coordination. Stewards will need to pay attention not only to species that are historically characteristic of a place, but also to other regionally native species that may be rare, or even currently absent from a place, but could thrive there with climate change. Since one location's outbound climate is another location's inbound climate (Hannah et al. 2014; Kling et al. 2024), nucleus-informed stewardship will necessitate coordinated management of both the nuclei as source populations and the sites receiving species dispersing from these nuclei. These origin and recipient sites will frequently occur across different management jurisdictions.

Climatic nuclei for native species could play important roles in applying the RAD (resist/accept/direct) framework for managers confronting ecosystem transformation (Schuurman et al. 2022; Lynch et al. 2021). For example, genotypic nuclei serve as seed sources to help maintain populations of foundational species, helping a regional ecosystem resist transformation under climate change. Climatic nuclei, in the absence of management intervention, may serve as local sources of native foundation species for emergent ecosystems. If those ecosystems have beneficial or desirable properties (e.g., ecosystem services, species habitat), the 'accept' option may be the most desirable alternative. Finally, active management aimed at directing change toward desirable new ecosystems can leverage climate nuclei, protecting them and utilizing them as propagule sources for transplantation across the broader landscape. In each of these cases, climate nuclei would be relevant for stewardship under climate change.

Protecting climatic nuclei of regionally native species may be particularly important in bolstering resistance to invasive species in future landscapes. Climate change-related species declines and extreme events may lead to sudden and extensive availability of space and resources. Both regional native biota and invasive species have the potential to exploit this resulting open niche space. Invasive species are likely to have a natural advantage here because of their typical capacity for rapid spread and establishment; many are projected to become increasingly aggressive competitors as climate changes (Jarnevich et al. 2014; Finch et al. 2021). The presence of native climatic nuclei, along

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with invasive species management, could increase the chances that newly assembling ecosystems resist the spread of invasives by fostering the presence of regionally native seed. In areas with high potential for invasion, or the presence of invasives that are outpacing the spread of regionally native focal species, direct planting using seeds or vegetative cuttings from nucleus populations may be needed.

While we have so far focused on the potential conservation value of climatic nuclei, nuclei that contain invasive species could accelerate the spread of these invasives with climate change. Some invasive species have yet to fill out their full climatic range (Bradley et al. 2015), but climatic nuclei could harbor populations of currently climatically restricted, but future successful, invasive species. Thus, environments that are likely to support climatic nuclei (e.g., Table 1) would be important locations to screen both for native species to promote beneficial spread and for invasive species to assess potential contribution to further invasion with climate change.

To begin to identify climatic nuclei, land stewards could use climate patterns, species patterns, or ideally, both. Some approaches to identifying nuclei could rely on natural history knowledge and basic climate data; others would likely require access to more sophisticated modeling efforts and may be more viable through land steward/research collaborations. Land stewards with strong natural history and botanic knowledge could identify climatic nuclei by locating where the most warm or dry adapted species (e.g., species that tend to grow in relatively more xeric climates) occur on the current landscape. These kinds of species would be concentrated in the warmest or driest environment within a landscape, as could be delineated on climate maps, and/or in the environments described in Table 1. Generally, if a stewarded area is located at the pole-ward or upper elevational edge of a species' range, it is likely to host climatic nuclei for the species. However, since species' geographic and climatic ranges do not always align (Oldfather et al. 2020), the more accurate way to identify an area likely to contain a species' climatic nuclei would be to evaluate whether the stewarded area falls at the cool or wet edge of a species' climate distribution.

Steward/researcher collaborations could model and visualize a range of futures for regionally native, high cultural and/or ecological value species, and identify which are likely to thrive under climate change in a stewarded area. Stewards could then look for the current locations of these species in or outside of the stewarded area to identify potential climatic nuclei. Alternatively, researchers could identify and map climate types—expanding, persisting, contracting, or novel climates (Williams et al. 2007; Ackerly et al. 2010) within and around a stewarded area. Climate analog methods facilitate measures of climate velocity—how fast each set of conditions is shifting across space (Hannah et al. 2014; Kling et al. 2024). Outbound velocities distinguish the speed at which species must move to track suitable climates. Inbound velocities, conversely, describe how fast species would need to move to arrive at a site of interest. Researchers could identify where projected analog climates for the stewarded area occur now (within or beyond its boundaries) (e.g., Figure 4). Depending on the ecosystem in question, a range of climate parameters could be used, including single metrics such as average annual temperatures, seasonal temperatures, precipitation, or multivariate climates. Land stewards could then explore the locations where a site's future dominant climates occur now to identify populations of species that may spread throughout or into the stewarded area in the future. In Figure 4 we use the Greater Yellowstone Ecosystem and Yellowstone National Park to illustrate this approach. Importantly, actual climatic nuclei can only be identified in retrospect, so monitoring will be a key piece of climatic nuclei conservation. Signs of a functioning nucleus would include increasing recruitment or survival within the nucleus and new recruitment beyond the nucleus.

Once identified, stewarding the climatic nuclei will involve many traditional strategies, such as invasive species removal, restoration or enhancement of habitat and ecosystem processes, and minimizing other threats. For example, in coastal California, at the mesic reaches of the endemic California buckeye (*Aesculus Californica*) distribution, isolated stands occur in pockets of xeric habitat—sheltered, south-facing river terraces with rocky soils—within mesic-associated coastal conifer forests (Calflora 2023, personal observation, authors). These stands might serve as climatic nuclei as the landscape becomes warmer and drier (Flint and Flint 2023). However, because of the prolonged absence of fire, Douglas firs are encroaching and limiting juvenile buckeye recruitment. To protect the buckeye nuclei, stewards could use intentional burning or other methods to clear encroaching firs.

From a species-level conservation perspective, outlier nuclei may represent areas disproportionately important to facilitating climate-adaptive range shifts, evidenced by paleoecological research on distributional responses to past climate changes and by studies of invasion biology (discussed above). Migration may happen most rapidly through dispersal from small outlying populations (Mack 1985; Clark et al. 1998). In expanding ranges, leading edge margin populations often possess traits for accelerated dispersal (Parmesan 2006). So, in addition to their value in landscape position, climatic nuclei may be particularly well-adapted to rapidly track novel conditions. Models that project future range shifts and include connectivity and dispersal parameters could help prioritize protection of those nuclei that contribute most to species capacity to track climate change. Practitioners tasked with conservation at regional or greater scales could consider the importance of outlier nuclei or climatic nuclei, particularly for range-restricted species, in broad land protection efforts such as 30×30 (Xu and Wang 2023).

Protecting genotypic nuclei could increase a population's genetic climate resilience. This approach is distinct from the climate adaptation strategy of 'assisted gene flow' (Aitken and Whitlock 2013), whereby potentially future climate adaptive genotypes are translocated to increase a recipient population's climate change resilience. The benefits of protecting genotypic nuclei (over long distance assisted gene flow), include maintenance of the integrity of local lineages and a reduced likelihood of importing maladaptive genotypes. However, genotypic nuclei would only function while local climate remained suitable for the genotypes represented in the nuclei, and protecting them may only be a temporary solution. Further, while genotypic nuclei may increase climate resilience for subpopulations in relatively mesic microenvironments, even more

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TABLE 1 | Environments that could support climatic nuclei under warming/drying climate trends (dependent on physiological and ecological constraints).

Potential Climatic Nuclei			
		WARM	**DRY**
Edaphic		**surface geothermal areas**	
Anthropogenic		**areas of low tree cover** higher temperatures	higher evapo-transpiration
Anthropogenic		**areas of low albedo (darker colors, coarser textures)** increased absorbed solar radiation and surface temps	higher evapo-transpiration
Hydrologic		**areas with lower subsurface water availability** reduced cooling from transpiration	reduced plant water available
Hydrologic		**areas with high snow accumulation** insulation from low winter temps	**areas with low snow accumulation** reduced meltwater
Topographic		**equatorial-facing slopes** higher solar radiation	higher evapo-transpiration
Topographic		**lower elevation locations** adiabatic lapse rate *but, can be associated with cold air pooling	orographic effects *but, can be associated with higher groundwater availability
Topographic		**coastal orientation** maritime warmer temperatures	**interior orientation** rain shadows
Topographic			**wind-exposed positions**
Topographic		**flatter slopes** higher insolation	**steeper slopes** thinner soils
Edaphic			**shallow soils**
Edaphic			**sandy soils**
Edaphic			**rocky outcrops**
Edaphic			**serpentine**
Anthropogenic		**mines** vegetation removal	topsoil removal
Anthropogenic		**urbanization**	
Anthropogenic		**areas cleared of tree cover**	

Note: Columns show potential warm (left) and dry (right) nuclei, with features that cross the center supporting both. Rows with a line separating right and left columns indicate an environment that would support warm nuclei in one form and dry nuclei in another. Blue shading indicates hydrologic, purple shading indicates topographic, yellow shading indicates edaphic, and grey shading indicates anthropogenic nuclei.

xeric-adapted genotypes (likely from other locations) would be needed to enhance the resilience of the genotypic nuclei subpopulation. For species that show local adaptation to climate across their range (e.g., Sork 2010, Lortie and Hierro 2022), assisted gene flow from the trailing range edge could complement genotypic nuclei protection. Genomic studies may help identify source populations well-suited to particular recipient populations (Mead et al. 2024).

Our recommendation to conserve climatic or genotypic nuclei as a climate adaptation strategy is offered in complement to a suite of other climate-forward conservation strategies (reviewed

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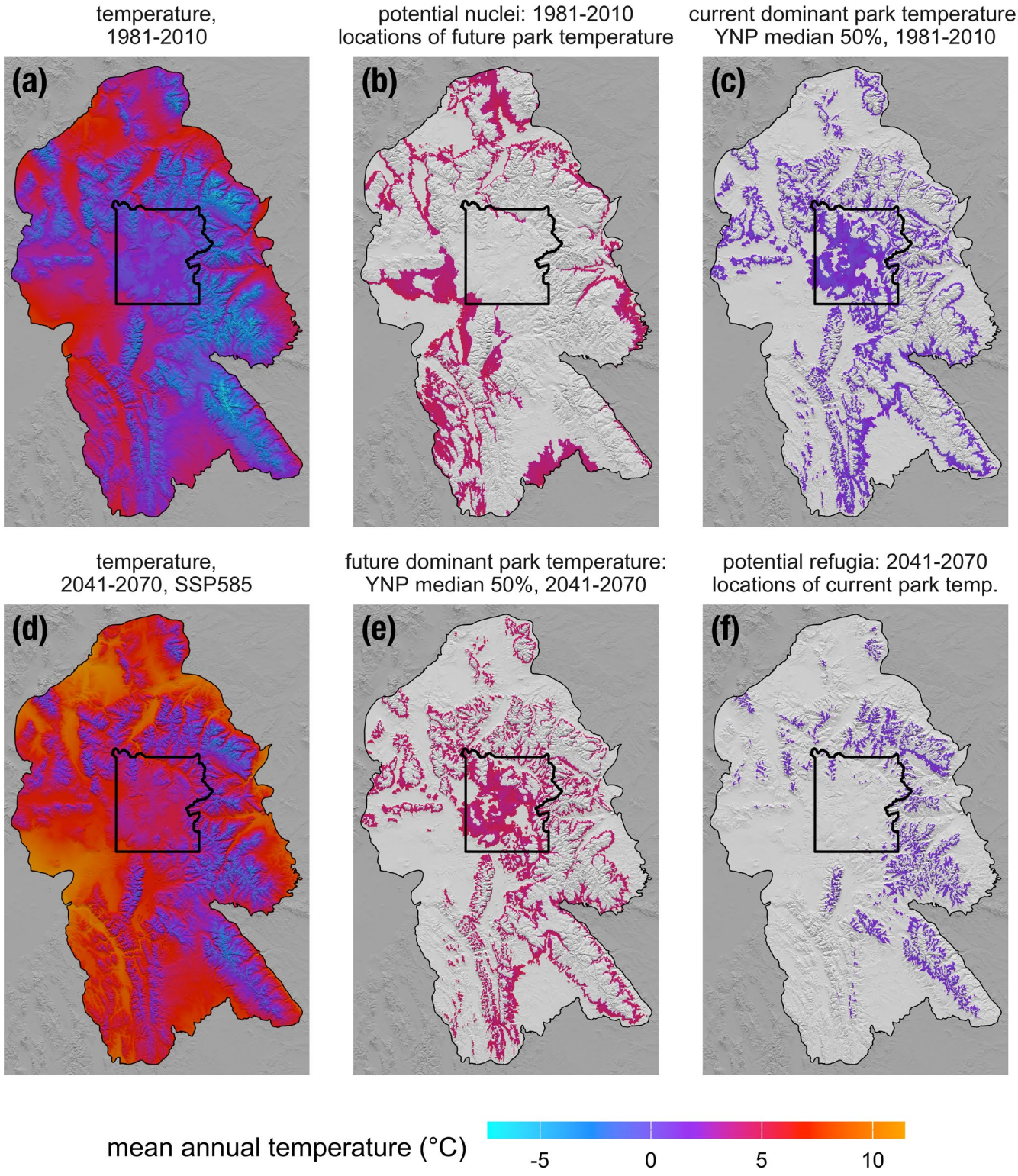

FIGURE 4 | Maps of the Greater Yellowstone Ecosystem, with the boundaries of Yellowstone National Park outlined in black. Panels (a, c, and e) show 1980–2010 baseline temperatures; (b, d, and f) show 2041–2070 future temperatures under a SSP585 scenario (representing the upper boundary of the range of scenarios described in the literature). Panels on the left show mean annual temperatures. Panel (c) shows potential climatic nuclei locations (pink) based on (d) the future dominant climates in the park (defined as the median 50% (IQR)). Panels on the right show (e) the current dominant climates in the park, and (f) the future locations of those climates.

in McLaughlin et al. 2022) For example, enhanced connectivity is essential for range shifts; climatic nuclei adjacent to significant dispersal barriers are less likely to play a substantial role in range expansion. In cases where populations cannot disperse to newly suitable habitat on their own (e.g., absent dispersers, climate change outpacing dispersal capacity, fragmentation, or established competitive invasives) human assistance would be necessary. Further, certain important population types are

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BOX 1 | Conceptual Stewardship Scenarios.

Climatic nuclei and stewarded areas:
To identify climatic nuclei, stewards could ask 'what species already occupy the hottest or driest sites in the stewarded area?' Or, more generally, 'what species are projected to increase, and where are those species currently located either within or near the stewarded area?' Models and maps of species climate futures could help identify species for which climate suitability is expanding, and likely locations of nuclei. However, local knowledge and field investigation will be critical to ground-truthing nuclei and assessing their conservation value

Nuclei inside stewarded areas:
In some cases, climatic nuclei occur within a stewarded area, where the future-thriving species are already part of the current local biota. An important management shift to support nuclei conservation would be to prioritize what might now be considered marginal and perhaps overlooked habitats and species. This could be challenging when nuclei are climatically unpleasant for human visitors, or do not contain historically iconic species

Nuclei outside stewarded areas:
Alternatively, species may spread into a stewarded area from climatic nuclei located outside the stewarded area's boundaries. In this case, to facilitate immigration, a cross-boundary approach would be needed to protect the nuclei, which would often occur near the warmer or lower-elevation edges of a protected area. Key needed shifts in conservation practice would include landscape level stewardship coordination (Scarlett and McKinney 2016) with areas beyond protected area boundaries to anticipate and facilitate incoming species; and an openness to stewarding regionally native species, even if they did not previously occur within the stewarded area

Climatic nuclei and species-level conservation:
A species-based approach to conserving climatic nuclei focuses on maximizing the climate resilience of a species across its distribution rather than the resilience of a given protected area. Here, outlier nuclei are particularly relevant because of their likely disproportionate influence on a species' ability to track rapid climate change. When high-resolution climate surfaces and species distribution data are available, mapping can allow for examination of which populations occupy the coolest or wettest areas of the climatic distribution (Chardon et al. 2015) and/or are climatic or geographic outliers. When available data are coarse, one could focus field reconnaissance at or just beyond the mesic edge of a species' known climatic distribution. Outlier nuclei may go unnoticed as nondominant parts of the landscape, but they might also garner attention precisely because they are rare and could be identified with the help of community science

unlikely to be conserved through climatic nuclei. For example, populations at a species' trailing range edge may already be declining with ongoing climate change—for these populations, conserving refugia and climate-adaptive genotypes for translocation would be critical. Conserving geologic and topographic diversity may enhance the climate resilience of a landscape by capturing refugia (Lawler et al. 2015). These surrogates also could capture nuclei; however, without consideration of focal taxa biology, they may miss key aspects of climatic nuclei conservation (Figure 2, Box 1).

5 | Future Research Directions

In this paper, we have outlined a heuristically simple version of climatic nuclei to spur discussion amongst practitioners and researchers. We hope others will critique and develop these ideas and apply them to additional landscapes and taxa. Research to support the application of the nucleus concept will need to delve further into the complexities of climate, physiography, community interactions, genetics, and life stages in determining nucleus-based range expansion. Field and modeling studies similar to those that have begun to identify the locations and function of climatic refugia could be applied to climatic nuclei. The development of high-resolution models and maps of species and communities under future climates could foster researcher/steward collaborations to identify potential climatic nuclei. Uptake and applied relevance of these research products require early input from all parties, availability in accessible formats, transparency around input data, plain language methods, and fully characterized and intuitively quantified uncertainty estimates.

Author Contributions

B. C. McLaughlin: conceptualization, writing – original draft, writing – review and editing. **M. M. Kling:** visualization, writing – review and editing. **S. T. Jackson:** conceptualization, writing – original draft, writing – review and editing. **E. S. Zavaleta:** writing – review and editing. **D. D. Ackerly:** conceptualization, writing – original draft, writing – review and editing.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data shown in figure 4 are openly available in Zenodo at https://doi.org/10.5281/zenodo.15358377.

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