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PERSPECTIVE

Inadvertent climate refugia

Forest P. Hayes[1] | **Joel Berger**[1,2]

[1]Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA

[2]Global Programs, Wildlife Conservation Society, Bronx, New York, USA

Correspondence
Forest P. Hayes, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523, USA.
Email: forest.hayes@colostate.edu

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Abstract
For centuries, humans have intentionally moved species around the world, and such actions have rarely been laudable from conservation perspectives. The notion that introduced populations of cold-adapted species hold conservation value despite their non-native status remains controversial. Many such populations exist as a legacy of humans moving wildlife to novel environments with little true consideration of species conservation. Herein, we identify cases in which individuals from inadvertent climate refugia (ICR) are returned to formerly occupied ranges or used to augment declining native populations. While conservation benefits have been infrequently realized, the global distribution of ICR offers a potentially untapped resource. Lessening biodiversity loss under increasing climate challenges will likely require assisted migration of many species and necessitate novel valuation of extant introduced populations—such as those within ICR. While ecological costs of translocated species are widely known, we highlight how species moved generations ago to ICR offer a reservoir for reintroductions and a buffer against rapidly changing climates.

KEYWORDS
anthropogenic, assisted migration, biodiversity, climate change, cold-adapted, conservation, mammals, reintroduction, translocation

1 | INTRODUCTION

Introduced organisms are rarely viewed as beneficial from conservation perspectives. However, amid unprecedented global change and loss of biodiversity, it is incumbent to consider if, how, and which populations may contribute to species persistence (Schlaepfer et al., 2011). As climate change threatens biodiversity, long-term conservation will increasingly depend on lessening global biodiversity loss through dramatic human interventions such as assisted migration (Table 1) (Hewitt et al., 2011). Among clear impediments to conservation are those associated with anthropogenic land conversion and habitat fragmentation, which, in turn, decrease the ability of species to make range shifts in pursuit of suitable biomes (Kuipers et al., 2021). Addressing biodiversity loss within communities occurring at high elevations and latitudes is especially pressing as they are among the most rapidly warming regions on Earth. Moreover, many cold-adapted species (Table 1) have reduced tolerance for high temperatures and are limited in geographic range (Abeli et al., 2018; White et al., 2018). If the status quo continues without strong intervention and innovative approaches to conservation, the result will be greater catastrophic losses of biodiversity.

Anthropogenic translocation of species to regions where they have not previously occurred has often been

TABLE 1 Operational definitions for key terms.

Term	Definition	Reference
Cold-adapted species	Species that occur and persist at high elevations and/or latitudes.	
	Although distributions of many cold-adapted species are limited to specific climatic conditions, others may be more broadly distributed at lower elevation or more southerly latitudes.	
Assisted migration	The purposeful movement of species to facilitate or mimic natural range expansion as a direct management response to climate change.	Vitt et al., 2010
	This term includes both translocation with the intent of hastening return or repopulation of a species within historic ranges and the translocation of species to areas outside their range.	
Climate refugia	An area or region that is large enough to sustain a population that provides suitable conditions for populations/species during periods of climate change.	Ashcroft, 2010
	These may include both in situ refugia (a subset of currently occupied areas) and ex situ refugia (areas with favorable habitat that were not previously occupied by the species). In this manuscript, we focus on refugia from anthropogenic climate change (i.e., as opposed to refugia during glacial or interglacial periods). We consider contemporary climate refugia to be areas providing suitable climate for population growth for species experiencing climate-related population declines elsewhere.	
Inadvertent climate refugia	An ex situ climate refugia established through anthropogenic translocation of a species without the intent of combating climate challenges	This paper

conducted exclusively for the benefit of humans (Long, 2003), with notable introductions of cold-adapted species to areas with favorable contemporary climates (Figure 1). If these populations are ecologically relevant for long-term conservation, then they must contribute either to range expansion or enhanced demographic security for the species at some point in time. Herein, we ask: have human-introduced populations of cold-adapted species yielded tangible conservation benefits for the natural populations of those species? In so doing, we emphasize there may be ecological or other costs beyond those of the species per se, but we concentrate on cold-adapted species for reasons we articulate below.

1.1 | Costs and opportunities of wildlife translocation by humans

Humans have a long history of translocating wildlife. Non-native species were first brought to Rome and Egypt around 2500 BCE. The first clear evidence of stocking wildlife per se was the delivery of 200 duck eggs within England in the 17th century (Leopold, 1933). Today, translocations of wildlife for hunting and agriculture are widespread, and agencies tasked with wildlife management routinely stock rivers and lakes with non-native species for recreational harvest. Humans have also introduced non-native terrestrial species globally (Figure 1). In places like New Zealand and South Africa, introductions have included wallabies (*Macropus* spp.), elk (*Cervus elaphus*), and hedgehogs (*Erinaceus europaeus*) (Long, 2003).

Human-assisted migration as a conservation strategy in response to global climate change has been on the public radar for several decades with deep consideration of potential trade-offs. Importantly, introduced species carry the risk of inimical interactions with native biota and, in the most problematic cases, may become invasive (Vitt et al., 2010). Conversely, introductions offer a means to thwart growing extinctions within native ranges and facilitate range expansion (Hällfors et al., 2017; Hewitt et al., 2011).

Decisions of species introductions must additionally consider the ecological impacts and weigh benefits against potential costs for other species. Does benefit to one species outweigh the cost to others or to strongly altered ecological processes? Are there alternative conservation actions, such as bolstering conservation within native ranges? Increasingly, quantitative approaches are being applied to balance values and determine the most beneficial approach (Yackulic et al., 2021). Answers to these questions are increasingly sought and require broader investigation.

At a species-specific level, assisted migration (Table 1) has been successfully used to restore populations to areas where they previously occupied. These include bison (*Bison bison*) and other charismatic vertebrates such as Arabian oryx (*Oryx leucoryx*) and gray wolves (*Canis lupus*) (Long, 2003; Sanderson et al., 2008). Importantly, most reintroductions are not conducted within a climate con-

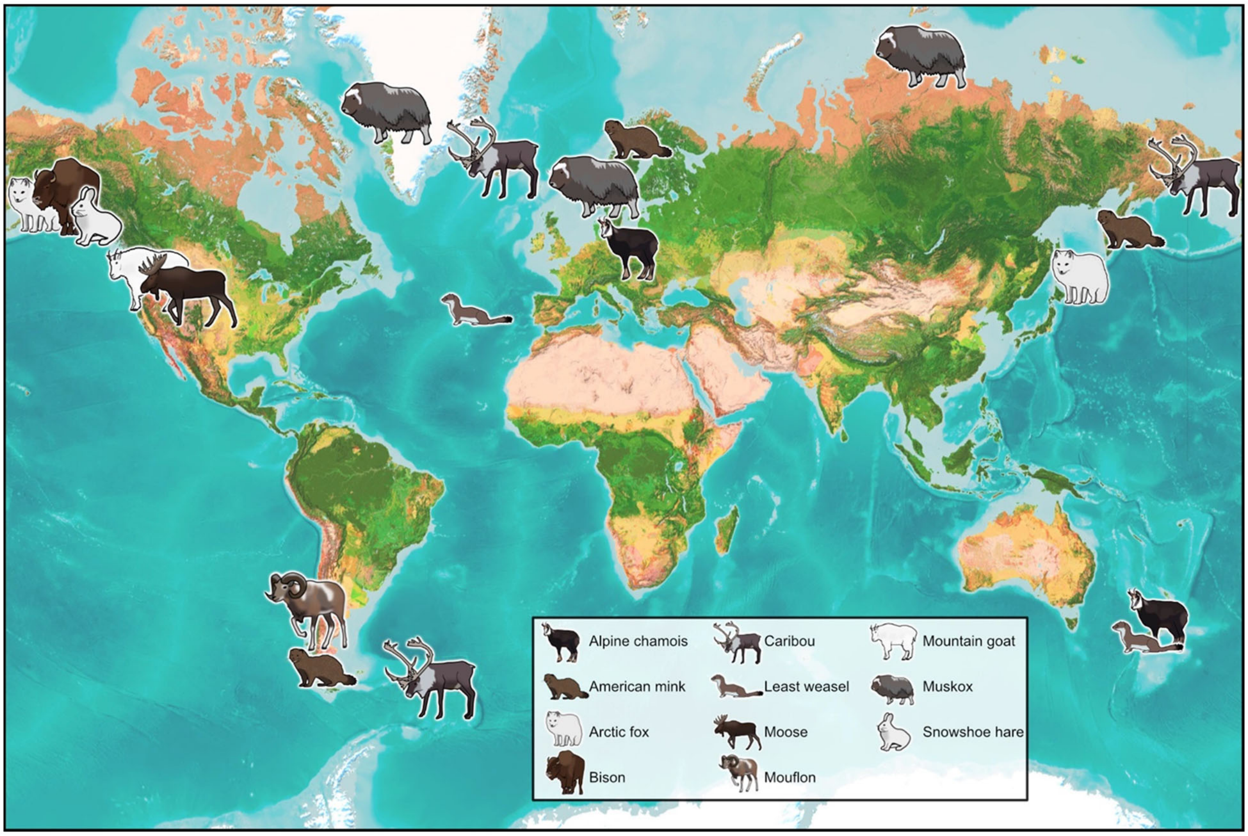

FIGURE 1 Humans have introduced many cold-adapted mammal species to geographies with favorable climates outside of native distributions. This figure highlights selected locations where introduced populations of cold-adapted species persist. Species, regions, and references are provided in Table S1.

text. Moreover, many reintroduced populations fail to successfully establish themselves, with fewer than half of historical reintroductions of those threatened or endangered species resulting in established populations (Fischer & Lindenmayer, 2000; Griffith et al., 1989). As ecoregions continue to shift due to climate change, attempts to maintain historical ecological baselines are increasingly difficult and, in some cases, may be counterproductive (Schlaepfer et al., 2011).

A prominent example of assisted migration to facilitate species persistence in the face of climate change involves cold-adapted trees where whitebark pine (*Pinus albicaulis*) were successfully translocated to higher latitudes to avoid extirpation under projected warming temperatures (McLane & Aitken, 2012). In a different case, Owens pupfish (*Cyprinodon radiosus*) were rescued from sure extinction—in a bucket—by translocation to a nearby riparian area (Pister, 2015). For species that are especially vulnerable to climate change, human-assisted migration is increasingly viewed as necessary for effective conservation of biodiversity (Hewitt et al., 2011; McLane & Aitken, 2012).

1.2 | Cold-adapted species

Like the whitebark pine example, cold-adapted organisms are fundamentally tied to areas of high elevations and latitudes. Even highly adaptable species of Holarctic distributions (e.g., moose; *Alces alces*) may experience thermal stress under moderate temperatures (Renecker & Hudson, 1990). In response to warming climes, some species are shifting to higher elevations and latitudes (Parmesan, 2006). As global temperatures continue to warm, with especially pronounced changes in montane regions, the persistence of numerous cold-adapted species within contemporary ranges will be challenged.

Historic range recessions and regional extirpations of cold-adapted species are well chronicled by fossil records from the warming Holocene, including from at least four mammalian orders—Artiodactyla, Lagomorpha, Rodentia, and Carnivora (respectively: mountain goat, *Oreamnos americanus*; pika, *Ochotona princeps*; marmot, *Marmota flaviventris*; and weasel, *Mustela nivalis*)—all from lower latitudes and elevations during cooler epochs where temperatures are now considerably higher (Hayes & Berger, 2023). The continued existence of these species of diverse taxa in isolated communities today indicates successful persistence within in situ refugia (Table 1) where acceptable climes endure. While this provides evidence of persistence during periods of warming, the rate of contemporary climate change far exceeds historical ones (Pörtner et al., 2021). Moreover, human land use has greatly reduced the habitat availability and connectivity for many species (Caro et al., 2022). The difficulty for contemporary cold-adapted species to respond to rapidly changing climates has prompted increased focus on proactive biodiversity conservation.

1.3 | Inadvertent climate refugia

Evaluation of contemporary climate refugia (Table 1) requires a nuanced assessment of both the climate threats to species and areas in which favorable climate conditions persist. For instance, has a species experienced climate-related population decline within its contemporary range? Does the species inhabit other areas with a more favorable climate? While refugia from anthropogenic climate change will be most accurately assessed through future retrospective analyses, affirmative answers to both of the above questions are indicative of contemporary climate refugia.

Climate refugia may exist far from natural populations making natural dispersal highly unlikely if not impossible. While assisted migration has been infrequently implemented as a conservation tool, many populations of introduced animals are found globally nowhere near their native counterparts. Such examples include beavers (*Castor canadensis*) from North America to Tierra del Fuego and Alpine chamois (*Rupicapra rupicapra*)—native to Europe and Anatolia—to New Zealand (Long, 2003). In North America, the introduction of mountain goats to Colorado, some at elevations exceeding 4000 m, is a case in point and has resulted in an expanded distribution at lower latitudes. We postulate that existing populations of species already introduced to ex situ climate refugia for reasons other than conservation may offer similar benefits for conservation as assisted migration. We term areas harboring these populations inadvertent climate refugia (ICR) (Table 1).

2 | WHAT IS THE CONSERVATION VALUE OF ICR?

Benefits that derive from populations within ICR have not been broadly evaluated and even realized gains have often been overlooked. Nevertheless, as efforts mount to sustain global biodiversity, it is fundamental to understand the potential conservation value of these populations. We suggest at least two benefits arise from species moved to ICR: (1) establishment of robust populations for species that are experiencing population declines within their historic ranges and (2) providing source populations and genetic reservoirs for species restoration. That said, these benefits do not exist in isolation, and we note introduction of species may carry additional unintended consequences, including disease exposure and supplantation of native species (Berger et al., 2022; Simberloff & Stiling, 1996).

While populations within ICR hold theoretical conservation value, we examined populations of cold-adapted species that have been introduced to high latitudes (Figure 1) to determine if any have realized conservation gains. Specifically, we investigated whether case studies exist wherein species have (A) native populations impacted by climate change, (B) populations within ICR, and (C) translocations from ICR that have restored or bolstered native populations (Figure 2). Below, we explore cases where three cold-adapted species—mountain goats, muskoxen (*Ovibos moschatus*), and bison—have been introduced and established for decades outside their historic range and where associated climates have supported population growth. For each species, we demonstrate clear conservation gains from ICR (Figure 3; see Table S2 for species' distributions, translocations, and climate challenges).

2.1 | Mountain goats

As an endemic to North America, this caprine is limited continentally to northwestern montane and periglacial regions (Hayes & Berger, 2023). Notably, they have been introduced at high elevations south of their native distributions where they have now colonized national parks (Grand Teton, Yellowstone) and to numerous locations in Colorado, Utah, and Nevada (Festa-Bianchet & Côté, 2008). Their strong association with periglacial regions and adaptations to cold have led to concerns about long-term persistence within their historic range.

Among the earliest introduction of the species to a novel environment was to the Olympic Mountain Range in Washington state during the 1920s, prior to the establishment of Olympic National Park. Mountain goats subsequently spread throughout the Olympic Mountains, raising concerns over ecological impacts on native communities. During 2018–2020, the park embarked on removing 90% of the introduced goat population. Of the removed individuals, 326 were relocated to areas in the Cascade Range where native populations of mountain goats were in low abundance due, in part, to anthropogenic activity (Harris et al., 2020). These translocations are an example of how an inadvertent refuge with a suitable climate has facilitated the restoration of the species within its native range.

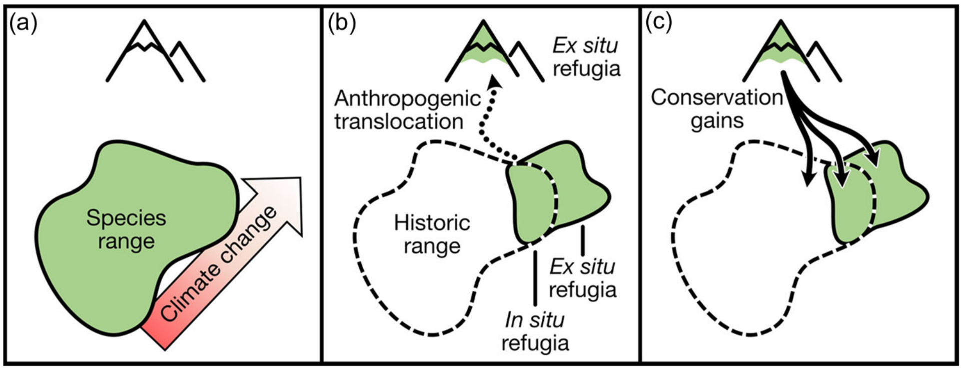

FIGURE 2 Species translocated to ex situ refugia offer reservoirs for conservation. Shaded areas (green) reflect inhabited range. (a) Climate change results in shifting of species' ranges in response to changing environmental conditions and habitat suitability. (b) Species that experience a decline in abundance or range may persist within in situ or ex situ climate refugia, including those established through anthropogenic translocation. (c) Introduced populations (e.g., from ex situ climate refugia) may yield conservation gains if they are translocated back to areas with extirpated or diminished populations.

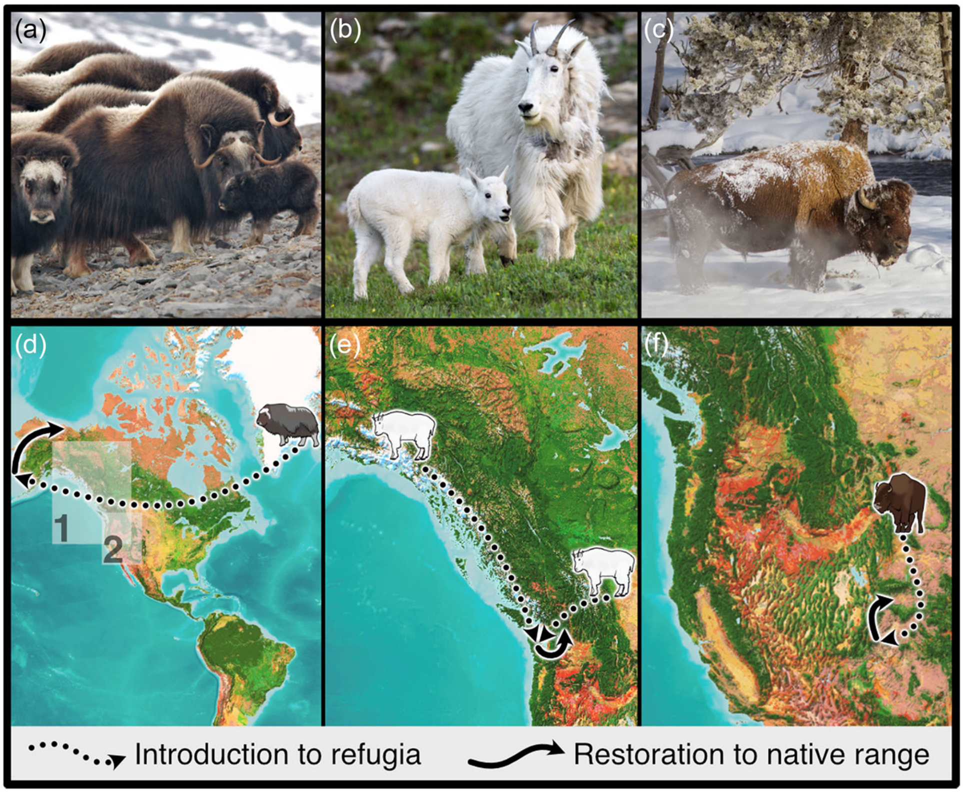

FIGURE 3 Examples of conservation successes arising from ex situ refugia. Introduced populations of (a) muskoxen, (b) mountain goats, and (c) bison have each facilitated restoration of native populations. Panels (d), (e), and (f) show the introduction to refugia and restoration to native ranges for each species. Inset (1) shows the map extent for mountain goats and (2) the map extent for bison. Photographs: (A) by J. Berger; (B) and (C) by F. P. Hayes.

2.2 | Muskoxen

Muskoxen are northern circumpolar in distribution, except in Europe, and primarily limited to Arctic tundra habitats (Cuyler et al., 2020). Historic populations were more broadly distributed but declined following the retreat of glaciers in the Holocene; the last native populations in Alaska were extirpated by the 1890s (Berger, 2018). Notably, muskoxen abundance is positively associated with cold and dry climate conditions, and they experience high mortality during extreme weather events, which are increasingly common.

In the 1930s, muskoxen were introduced outside their modern native range to Nunivak Island in western Alaska. Because they had been hunted to extinction in Alaska, the intent was to reintroduce the species for hunting and for food. The population on Nunivak grew steadily and stabilized at ~500 individuals. The Nunivak founders have now been reintroduced to other areas of Arctic Alaska with all ~4000 muskoxen descended from the single introduction outside their native range (Cuyler et al., 2020). The deliberate initial restoration of a population beyond its natural range now typifies the high-potential conservation value of an ex situ climate refuge.

2.3 | American bison

The case involving bison is more nuanced because of broadscale anthropogenic reductions in population size across much of North America by human hunting (Sanderson et al., 2008). Today they occur as geographically isolated populations. In 1941, bison were transplanted from Yellowstone National Park to higher elevation outside their historic native distribution to the Henry Mountains, a montane island jutting above Utah deserts to more than 3500 m (Van Vuren & Bray, 1986). The introduction to Utah was to establish a harvestable population as there was no evidence that they previously occupied the region.

Relevant from a conservation perspective, bison from the introduced Henry Mountain population were translocated decades later back to native areas on the Uintah and Ouray Reservation by the Ute Indian Tribe in northern Utah (Utah Wildlife Board, 2007). This reintroduction—from a higher elevation climate refuge—has aided in the continued restoration of the species with high cultural value for native indigenous and other Americans. As efforts mount to expand the restoration of the species to formerly occupied reaches, the presence of multiple source populations will facilitate this endeavor.

3 | THE FUTURE VALUE OF ICR

As climate change alters the location of suitable habitats for many species, changes in biotic communities are inevitable (Schlaepfer & Lawler, 2023). Climate refugia will play a key role in determining future distributions whether species are rare, threatened, or otherwise declining (Ceballos & Ehrlich, 2002). Concurrently, restoration of diminished or extirpated populations will become increasingly difficult and less likely to succeed (Thorpe & Stanley, 2011), except perhaps to the more climate-appropriate parts of ranges or to ex situ climate refugia (Marchetti & Engstrom, 2016). Such introductions necessitate serious planning discussions, as has been the case for whitebark pine and certain extensions for cold-adapted fish (Harig et al., 2000; Pister, 2015). ICR have netted conservation value for a few large mammals (Figure 3), but for many organisms vulnerable to warming temperatures, translocation has only recently become part of broader discussions.

Despite clear conservation value, much trepidation persists about assisted migration and the consequences of non-native species (Hewitt et al., 2011). Caution is warranted as introductions of Burmese python (*Python bivittatus*), for example, have decimated local native mammalian biodiversity (Guzy et al., 2023), although the species was not introduced for ecological benefit. While the majority of introduced species may not be highly disruptive (Simberloff & Stiling, 1996), we must be mindful of balancing the status of already climate-stressed native species where species are introduced for their ecological benefits.

Although we have identified unforeseen conservation benefits from multiple populations of introduced cold-adapted species, whether those populations should be fostered will require greater investigation of the cost to other species. For example, the restoration of mountain goats (Figure 3) was conducted, in part, to reduce impacts on sensitive vegetation communities (National Park Service, 2018). Additionally, it should be considered that alternative actions (e.g., translocation from a population with greater genetic differences) may confer even greater benefits.

Fundamentally, management and conservation of wildlife is a values-based decision process with costs and benefits associated with any action. Although assisted migration has been circumspectly implemented, innumerable translocations have already taken place, often without conservation intent (Figure 1) (Long, 2003). Additionally, large-scale environmental changes increasingly make strict maintenance of historical ecological baselines untenable (Schlaepfer & Lawler, 2023) and fuel discussions about the nature of ecological surrogates to replace native species that have experienced localized extirpation (Lundgren et al., 2024). Thus, future conservation success will depend on reconciling values with these ecological realities and differences in philosophical bent.

As Earth's climate continues to warm, there is a clear need to nurture the changing compositions of biotic communities. Populations within ICR offer promise for long-term species persistence while reducing the need for assisted migration. To date, the conservation potential of these introduced populations is largely untapped in efforts to mitigate unprecedented climate challenges and loss of biodiversity (Gibson & Yong, 2017). Of course, the broader conservation value must also be weighed against impacts on local biota on a case-by-case basis. Regardless, efforts to slow biodiversity loss will increasingly warrant extraordinary measures and multifaceted solutions wherein ICR may play an important role.

While our work focuses on cold-adapted species at high latitudes, we can easily envision ICR being more broadly applied under different suites of thermal conditions. For instance, climate change threatens the persistence of some small mammals on low-lying coastal islands (Boone & McCleery, 2023). For such species, more interior regions with similar thermal conditions may offer climate refugia. Therefore, as climate change has sweeping effects on species within all biomes, climate refugia and, perhaps, ICR may play critical roles in the persistence of far more species than just cold-adapted ones.

ICR and populations contained within offer great potential for applied conservation. We have highlighted not only the anthropogenic creation of ICR for cold-adapted species but also identified realized conservation benefits for at least three cold-adapted mammals (Figures 2 and 3). There are certainly additional cases in need of reporting and debate, but the more pressing issue for future generations is how to structure realistic plans for the management of biological diversity and ecosystem function amid rapid climate change (Berger et al., 2022; Schlaepfer & Lawler, 2023). Future conservation may be greatly benefited not only through the mindful translocation of species with conservation intent but also through increased recognition of the potential value of existing non-native populations.

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DATA AVAILABILITY STATEMENT

All relevant data are provided within the main body of this manuscript or as supporting information.

ORCID

Forest P. Hayes https://orcid.org/0000-0002-7216-5360

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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