Research Topics

Rewilding in practice

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Rewilding in practice

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Editorial: Rewilding in practice

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Editorial on the Research Topic
Rewilding in practice

Rewilding, at its core, is not a one-size-fits-all endeavour; its success depends on a range of factors from local ecological dynamics to socio-economic considerations, and it follows that there is a need for grounded, context-specific approaches. The case studies presented in this Research Topic provide a nuanced lens through which to explore the interplay of variables unique to each rewilding project. By focusing on specific examples, researchers and practitioners can glean invaluable insights into what works, what doesn't, and more importantly, why rewilding was the chosen approach. This provides us with essential knowledge for steering future rewilding projects.

Case studies offer a platform for holistic assessment, ranging from the efficacy of monitoring approaches (Cowgill et al.) to broader socio-cultural dimensions (Root-Bernstein and Guerro-Gatica). They illuminate the multifaceted impacts of rewilding on local communities, economies, and cultures, shedding light along the way on both potential benefits and unintended consequences. Such insights are valuable for fostering genuine collaboration, but also for ensuring that rewilding initiatives are not only ecologically sound, but also socially equitable and sustainable.

Understanding the adaptive capacity of rewilding strategies is vitally important. Rewilding is a long-term process, so documenting change over time is important to both monitor change on the ground while providing vital insight to inform rewilding guidelines and frameworks. Here, case studies serve as living laboratories; showcasing real-world responses to evolving environmental, economic and social pressures. Rewilding itself is a changing concept and has adapted over time. As the case studies in this Research Topic demonstrate, the primarily ecological focus of rewilding has expanded to reflect paradigm shifts in wider conservation towards eco-cultural or social-ecological systems approaches. Ecologically, rewilding denotes a paradigm shift from compositional towards functional restoration. The governance and cultural implications of this more indeterminate approach, including adaptive co-management, human dimensions and human-nature connections, are addressed in practice and in theoretical frameworks in many of the contributions to this Research Topic.

Tracking the long-term outcomes of rewilding interventions—from the 'spontaneous rewilding' of natural recolonizations to more interventionist translocation approaches—provides invaluable insights for adaptive management, as illustrated by these and other case studies on impacts on ecosystem or social-ecological system persistence and resilience. This is a crucial tool for navigating (and indeed accepting) uncertain ecological futures wherein nature takes more of leading role.

Documenting case studies is not merely a supplement to rewilding initiatives; it is a fundamental component of rewilding success (or failure). By grounding project ambitions in tangible realities, case studies provide the foundation needed for successful project management and in doing so unlock a wilder, more resilient future for all. Rewilding may carry distinct meanings and nuances in different languages and cultures, and below we explore how rewilding is understood across various linguistic and cultural contexts. Understanding these meanings and definitions and how they differ across geographies can help us identify and compare best practices and lessons learned (Hertel and Luther).

The interpretation of rewilding can vary significantly across cultures and languages. The term is associated with the notion of wilderness, which in itself lacks a specific word or translation in many languages, and whose understanding depends on the socio-ecosystems in which it is embedded (Locquet and Héritier, 2024). While it universally implies encouraging the return of autonomous processes within and across ecosystems, the specific approaches, priorities, cultural perspectives, and limitations of rewilding can differ based on local contexts and values. Understanding these diverse meanings is crucial for effective cross-cultural dialogue and collaborative conservation efforts worldwide, and for understanding some of the situated practice explored in the papers in this Research Topic.

In Spanish, the notion of rewilding is translated by the term *resilvestración* (FundéuRAE, 2019), composed of the prefix *re* and the adjective *silvestre*, which refers to natural non-cultivated plants or non-domesticated animals (FundéuRAE, 2019). This term is commonly used to describe rewilding efforts, underscoring the restoration of ecosystems, and focusing on the recovery of natural processes and the revitalization of biodiversity.

In French, rewilding is often translated by "renaturation" or "restoration," which are often used interchangeably (Dehaut, 2023); these notions are based on definitions that are not completely stabilized (Barraud, 2007). The concepts of renaturation and restoration are also generally associated with interventionist practices, or ecological engineering, and with fixed reference states, which differs from rewilding approaches. The concept of "*renaturalisation*" or "*renaturalización*" (also used in Spanish to translate rewilding) is mainly associated with actions carried out in urban environments or on watercourses after phases of major anthropisation to restore natural dynamics (Pech, 2016). Indeed, this term is found in most Latin languages such as *'renaturalização'* (Portuguese) (Pereira et al., 2010) or *'rinaturazione'* (Italian) (Brambilla, 2019). Rewilding can also be translated in French as *'réensauvagement'* (Cochet and Kremer Cochet, 2020; Barraud, 2021; Faure, 2023), which is often understood as the return of 'savage' (i.e., wild) entities and predators. Here it has a negative connotation and is also associated with a form of appropriation of territories by groups of external stakeholders. In Portuguese, rewilding can also be translated as *'refaunação'*, referring to wildlife reintroduction.

In German, rewilding is translated as *"Wiederansiedlung von Wildtieren"* or *"Wildnisentwicklung."* These terms emphasize the reintroduction of wild animals and the promotion of wilderness development. In Japanese, rewilding can be interpreted as "自然再生" (*'shizen saisei'*) or "野生復帰" (*'yasei fukki'*), where these terms emphasize the regeneration of nature and the return of wildness to landscapes. Although there are terms in different languages to try and translate rewilding, the word is often found as it is, in English, in scientific literature, regardless of the language employed.

In China, the term eco-civilization refers to the sum of material, spiritual, and institutional achievements made by human beings for protecting and building a beautiful ecological environment, and it is a social form in which people and nature, environment and economy, and people and society coexist in harmony (Zhou, 2012; 2021). Cao et al. (2022) note that there are 'well-documented social, economic, cultural, and ecological benefits of rewilding that align with eco-civilization and the broader sustainable development agenda' while also noting the challenge of effectively communicating, translating, and integrating the philosophy and science of rewilding and eco-civilization, while also staying true to the ethos and origins of both concepts.

Over the years, rewilding has been adopted and adapted in various contexts, earning it the label of a "plastic word" due to its broadened scope beyond the initial meaning of "to make wild again" (Jørgensen, 2015). Language naturally evolves, with words often retaining old meanings while acquiring new ones (Jørgensen, 2015). Specifically for rewilding, its usage now spans wider ecological and cultural dialogues, resonating with numerous viewpoints from scientists to environmental advocates.

Rewilding has largely focused on Europe and North America, but there are continental differences in rewilding thinking and practice. The social context for conservation and land management is significantly different between continents; thus, issues related to governance, Indigenous rights, and traditional land uses that are place-specific should be taken into account, as well as how rewilding in itself is defined and understood (Root-Bernstein et al., 2017).

Rewilding in Australia, for example, has developed a distinctive approach, shaped by the continent's unique ecosystems, biodiversity, and historical context. Here rewilding focuses on restoring small to medium-sized native mammals rather than apex predators, reflecting its ecological challenges. Species like bilbies, bettongs, and numbats have declined due to predation by invasive species (e.g., foxes, cats), habitat loss, and altered fire regimes. Rewilding projects address these issues by creating predator-free reserves and reconnecting fragmented habitats. Initiatives by organizations like Australian Wildlife Conservancy (AWC) and Arid Recovery have reintroduced species such as the western quoll (*Dasyurus geoffroii*) to areas like the Flinders Ranges, helping restore ecological balance. In Australia, as elsewhere, few

Indigenous community-led restoration projects are identified as rewilding, which might imply a withdrawal of people or their practices from traditional lands (Bartel et al., 2021). More often, such restoration projects are described in terms of healing Country or caring for Country, emphasizing the reliance of such places on the people that belong to them (Rose, 1996). Conservation best practice demands that ecologists partner with Indigenous communities to integrate traditional land management practices, like cultural burning, to maintain habitat diversity and reduce wildfire risks.

This blend of conservation science and Indigenous knowledge highlights a unique approach, emphasizing ecosystem resilience and sustainability. Perceptions of rewilding as 'hands off' or promoting human withdrawal conflicts with Indigenous Australians' ecological custodianship (Bartel et al., 2021), and therefore aligns more with rewilding as more-than-human collaboration and coexistence (Hawkins et al., 2024).

Africa stands out for its rich variety of large herbivores and predators, which are crucial in maintaining its ecosystems. However, rapid human population growth has caused a surge in the encroachment of wildlife habitat, hunting/poaching for 'bushmeat,' and intensified human-wildlife conflicts, presenting significant challenges for conservation and rewilding efforts. African rewilding initiatives focus on expansive ecosystems and iconic species, such as elephants, rhinos, big cats, and wild dogs. These large animals require extensive, well-connected habitats; thus, rewilding emphasizes restoring and protecting vast, interconnected landscapes, like the Niassa-Selous wildlife corridor, which links major conservation areas in Mozambique and Tanzania (Niassa-Selous Transfrontier Conservation Area, n.d.)

Addressing human-wildlife conflict and encouraging coexistence is essential. Such conflicts frequently stem from crop damage, livestock losses, and risks to human safety. In Kenya's Maasai Mara region, strategies to mitigate conflicts with elephants include engaging local communities, establishing barriers, monitoring elephant movements, and deploying rapid response teams. These initiatives seek to minimize retaliatory killings and promote coexistence between humans and wildlife (Mara Elephant Project, n.d.).

Where wildlife has been depleted, reintroduction is a key rewilding strategy. In Mozambique's Gorongosa National Park, large mammals that were totally or nearly extirpated by years of civil conflict, such as wildebeest, buffalo, leopards, and wild dogs, have been successfully reintroduced, helping to restore the park's ecosystem (Pringle and Gonçalves, 2022).

Rewilding can also involve the restoration of lost abiotic processes. For example, the Waza-Logone floodplain (Moritz et al.) was reflooded to benefit humans and wildlife. Nonetheless, despite its promising potential, insufficient security and investment in Waza National Park have hindered the recovery of wildlife populations, although local communities have benefited.

Many African conservation and rewilding projects integrate local communities, addressing human and ecological needs within a socio-ecological framework. Initiatives like Kenya's Northern Rangelands Trust involve local communities in habitat restoration, ensuring socio-economic benefits alongside ecological gains (Northern Rangelands Trust, n.d.). Indigenous knowledge, including traditional fire and grazing management, is increasingly integrated to maintain ecosystem health. This combination of restoration and community engagement presents rewilding as not only an ecological goal but also a strategy for sustainable development, conflict resolution, and cultural preservation.

Rewilding in South America is defined by the continent's vast and diverse ecosystems, ranging from rainforests and savannas to wetlands and grasslands. The distinction between rewilding and species reintroduction, however, is not always clear (Root-Bernstein et al., 2017). Efforts primarily focus on restoring native species and ecosystems that have been impacted by deforestation, habitat fragmentation, and agricultural expansion. A prominent example is the Iberá Rewilding Project in Argentina, where species such as jaguars, giant anteaters, and red-and-green macaws have been reintroduced to revive the ecosystem after decades of degradation. This project, led by Rewilding Argentina, highlights the potential of rewilding to restore apex predators and keystone species, which help maintain ecological balance.

A unique aspect of South American rewilding is the emphasis on large-scale, landscape-level restoration. For instance, rewilding projects in Chilean Patagonia, like the Pumalín and Patagonia National Parks, have focused on restoring ecosystems affected by overgrazing and unsustainable logging practices. In Brazil, Refauna is a network of universities, organizations, zoos, and breeding facilities, working together since 2010 on the Atlantic Forest's restoration through reintroduction of key species like the tapir, the howler monkey, the tinga tortoise, and the red agouti. The network is currently present in more than 120 protected areas in the biome. Significant efforts have been directed to restoring (or rewilding) the Tijuca urban Forest in Rio de Janeiro. Rewilding in South America often involves collaboration with local and indigenous communities, and small-scale farmers. Projects like these not only seek to restore biodiversity but also aim to create sustainable economic opportunities through ecotourism, reinforcing the connection between ecosystem health and community well-being.

Rewilding in Asia takes diverse forms, reflecting the continent's vast range of ecosystems, cultural landscapes, and conservation challenges. For example, the success of various tiger (*Panthera tigris*) translocation initiatives in India has not only protected the tigers but has also reinforced the entire ecological web that depends on them, leading to healthier forests and increased biodiversity. Dutta and Krishnamurthy (2024) report on the Panna Tiger Reserve in Central India and note that (a) the presence of tigers helps regulate prey populations and contributes to overall ecosystem stability; (b) tiger conservation necessitates the protection of large, contiguous habitats, benefiting many other plant and animal species; (c) healthy ecosystems are able to provide ecosystem services such as water purification, carbon sequestration, and climate regulation; and (d) tiger conservation can also stimulate ecotourism, generating economic benefits for local communities and supporting further conservation efforts.

Lamperty et al. (2023) view Singapore as 'a natural rewilding experiment as large mammals that were extirpated in the last century have begun to recolonize the island, partly due to Singapore's successful regreening efforts.'

Drawing on a case study of rewilding and avian diversity and endemism in the Sanjiangyuan region of the eastern Qinghai-

Tibetan Plateau, Li et al. (2018) challenge the assumption that reducing human impact invariably leads to biodiversity gains. Whilst rewilding can (depending on context) support high avian species abundance and diversity, rewilding outcomes are not always predictable and depend on the specifics of the landscape and the species involved. Passive rewilding does not necessarily guarantee positive biodiversity outcomes. They conclude that rewilding efforts should carefully review ecosystem service and biodiversity objectives, emphasizing the need for a nuanced, site-specific approach that considers the historical interaction between humans and the landscape, maintaining a balance between ecosystem services and the protection of unique biodiversity.

In China, while the concept of "rewilding" is still developing, many conservation practices already align with the 3C model. The establishment of national parks exemplifies core area conservation, with strict management ensuring ecological integrity (Zhao, 2022). The Giant Panda National Park is a prime example of connectivity conservation, linking numerous nature reserves into a vast habitat network, with a dedicated corridor plan to enhance connectivity (Swaisgood et al., 2023; Yang et al., 2020). Efforts also focus on reintroducing key species, such as the snow leopard (Alexander et al., 2016) and North Chinese leopard (Yang et al., 2021).

In Southeast Asia, rewilding is often linked to rainforest restoration, where reforestation projects work to rehabilitate ecosystems damaged by palm oil plantations, logging, and agricultural expansion. The Hutan Harapan Ecosystem Restoration Concession (ERC) in Sumatra, Indonesia is a potential model for 'rewilding lite' approaches for restoring degraded lowland rainforests (Utomo and Walsh, 2018). Hutan Harapan has been significantly degraded by past logging, but still retains high biodiversity value, including globally threatened species. The ERC framework legally designates production forests for restoration and conservation, rather than just timber extraction, while also restoring degraded areas through sustainable practices like agroforestry and non-timber forest product harvesting. This holistic approach addresses both ecological and socio-economic goals and demonstrates that areas managed for multiple objectives can contribute significantly to biodiversity conservation. As a note of caution, however, the Indonesian Omnibus Law of 2021 has changed the role of Ecosystem Restoration Concessions, and they are now treated the same as forest licenses that are not intended for conservation, and challenges such as illegal encroachment (e.g., oil palm plantations), forest fires, and financial sustainability continue to be a problem.

In addition to the difficulties of translating and understanding the term "rewilding," it appears that not all stakeholders use this word. It is mainly used by international organizations (e.g., Rewilding Europe or the Global Rewilding Alliance), which contribute to spreading a model of practice, and in scientific literature. For example, in France, the word is rarely used by managers, either in its French or English versions, and because of the diversity of socio-ecological contexts, other concepts are emerging. Here it is the notions of "*libre évolution*" and "*naturalité*" that are most commonly used.

The examples of rewilding in this Research Topic range from Community Case Studies focusing on consensus and alliance building (Root-Bernstein and Guerro-Gatica), reflooding and its different impacts on human and wildlife populations (Moritz et al.), and the integration of Indigenous knowledge, ceremony, and cultural monitoring in reintroduction efforts (Heuer et al.), to Systematic Reviews on trends for monitoring terrestrial rewilding with environmental metabarcoding (Cowgill et al.) and the evolution of the Yellowstone to Yukon initiative (Hilty et al.). Hertel and Luther argue that rewilding success hinges on both ecological and sociopolitical factors. Local awareness, proof of concept, and recognizing species' intrinsic value are crucial for maximizing success in future projects. In the Original Research section, we delve deeper to develop learning from a broad set of case studies into rewilding guidelines and a theory of change for rewilding application (Hawkins et al.), while a case study of a cheetah reintroduction in Namibia highlights the importance of understanding environmental settings and animal history and behavior for rewilding and ecosystem restoration (Dimbleby et al.). Finally, Jones and Jones, in the Policy and Practice Reviews, provide a comparison of the principles for rewilding as an approach to ecological restoration with IUCNs principles for Nature-based Solutions in the context of beaver reintroductions in the UK.

This Research Topic underscores the vital role of meaning and context within rewilding efforts. The diverse range of topics, highlighted by examples from various continents, illustrates that rewilding is a complex undertaking shaped by socio-economic and cultural factors, in addition to ecological considerations. As rewilding continues to advance and transform, documenting and learning from these experiences remains crucial. As Eileen Crist (2024) recently observed, the focus has shifted beyond 'the great wilderness debate' to confronting a world increasingly characterized by a 'human monoculture' on a trajectory toward a 'profitable apocalypse.' Around 75% the planet's land surface is experiencing measurable human pressures (Venter et al., 2016). Now, more than ever, it is essential to advocate for a hopeful and positive vision of rewilding to safeguard the future of our planet.

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Reintroducing bison to Banff National Park – an ecocultural case study

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The reintroduction of extirpated species is a frequent tactic in rewilding projects because of the functional role species play in maintaining ecosystem health. Despite their potential to benefit both ecosystems and society, however, most well-known species reintroductions have adopted an eco-centric, "nature-in-people-out" approach. Rewilding theory and practitioners acknowledge that ignoring the role Indigenous people did and might once again play in shaping the distribution, abundance, movements, behavior, and health of wild species and ecosystems, is limiting. In this case study, we describe the technical steps we took and how Indigenous knowledge, ceremony, and cultural monitoring were woven into the recent reintroduction of plains bison to Canada's Banff National Park. Six years later, the reintroduced bison herd has grown from 16 to >100 animals, ranges mostly within 30 km of the release site, and, if current growth continues, will likely be managed with Indigenous harvesting. Transboundary bison policy differences are shifting and may lead to bison being more sustainable. The ecocultural approach, therefore, has increased the resilience of our rewilding project.

KEYWORDS

rewilding, reintroduction, ecocultural, indigenous people, threatened species, plains bison, *Bison bison bison*

1 Introduction

Rewilding is a bold, often costly, ecological discipline aimed at reversing biodiversity loss and climate change. Strategies typically include reintroducing species in the hope that the return of ecological processes they facilitate, like dispersal, competition, predation, and mutualism, leads to broader ecosystem restoration (Bakker and Svenning, 2018; Perino et al., 2019; Svenning, 2020; Schmitz et al., 2023). The discipline, however, has been criticized for excluding local people's current and past roles in stewarding and shaping nature (Jørgensen, 2015; Martin et al., 2021; Massenberg et al., 2023). This may be due to practitioners' view that people are the cause of most ecological problems (Marris, 2011) but such generalizations tragically overlook the role of Indigenous practices, like hunting (Hessami et al., 2021; Farr and White, 2022) and burning (White et al., 2011a; Hoffman et al., 2021) in creating and perpetuating the very ecosystem conditions we aspire to rewild (Fuhlendorf et al., 2009; Kimmerer, 2013). As the following case study of returning plains bison (*Bison bison*) to Banff National Park, Canada (BNP) illustrates a more holistic "ecocultural" approach that explicitly engages human communities and restores ecologically beneficial cultural practices, can lead to greater and more resilient rewilding outcomes (Figure 1). Other studies have highlighted the benefits of engaging local communities (Zamboni et al., 2017; Pettersson and Carvalho, 2021) but for brevity we focus specifically on the benefits of interweaving Indigenous with Western scientific knowledge in this case study.

Plains bison are ideal candidates for ecocultural rewilding: they are a keystone species and ecosystem engineer that greatly influences ecosystem processes like energy flow and nutrient cycling with their extensive grazing, wallowing, trampling, herding and migratory behaviors (Hobbs, 1996; Knapp et al., 1999; Olson and Janelle, 2022), and they are of great cultural importance to North American Indigenous plains cultures for food, clothing, lodging, and spiritual foundations (Isenberg, 2000; Aune et al., 2017; Shamon et al., 2022; Figure 1). This changed abruptly between 1860 and 1885 when tens of millions of the animals were hunted to the brink of extinction across the Great Plains, foothills, and front ranges of North America's Rocky Mountains (Roe, 1970; Shaw, 1995), largely with the colonial intent to destabilize and remove the independence of Indigenous groups, who relied on bison, so their historic homelands could be more easily settled (Brink, 2009). Ironically, the Canadian government helped rescue plains bison from extinction around the same time as it pushed this colonial agenda. It purchased several hundred descendants of the last wild bison from two Montana ranchers and shipped them to Elk Island National Park, Alberta, and beyond in 1907. This started a 100+ year legacy of bison conservation in Parks Canada, whereby offspring from that herd, which are considered one of the purest genotypes of wild plains bison in the world, have been used to seed new populations in Prince Albert and Grasslands national parks, and dozens of other sites, including the one in this case study (Locke, 2016; Markewicz, 2017).

Although more than 500,000 plains bison now exist in North America, only 4% are managed for conservation (Freese et al., 2007). The remaining 96% of bison are managed within a ranching industry where selection for weight gain, ease of handling, and fecundity continues to alter the bison genome (Stroupe et al., 2022). Of the bison managed for conservation, fewer than 8,000 roam free of fences, and only across <1% of their historic range. Most (~5,000) are in the Yellowstone area; the rest are in four isolated herds of a few hundred to over one thousand animals that are functionally disconnected from one another (Sanderson et al., 2008; Farr and White, 2022). As a result, plains bison are listed as Near Threatened on the IUCN Red List (Aune et al., 2017).

The greatest barriers to their recovery are the lack of large intact landscapes (COSEWIC, 2013; Farr and White, 2022), social intolerance (Clark et al., 2016; Jung, 2020), perceived competition with other ungulates (Jung et al., 2018), potential disease transmission to livestock (White et al., 2011b; Kamath et al., 2016), and concerns over property damage and human safety (Sanderson et al., 2008). Banff National Park (BNP), on the northwestern edge of historic plains bison range (Allen, 1876), is free of many such barriers and was recognized as a rare opportunity to restore only the fifth free roaming, unfenced population of plains bison in the world (White et al., 2001). The area, which was protected as the world's second national park in 1885 and is part of a 23,600 km^2 World Heritage Site (IUCN, 2020) is big, mostly intact with healthy populations of grizzly bears (*Ursus arctos*) and is, wolves (*Canis lupus*) and all other native fauna except caribou (*Rangifer tarandus*) (Hebblewhite et al., 2010). It is also is free of conflicts with domestic livestock (the nearest cattle graze ~20-50 km away), and is governed by a mandate to maintain and restore ecological integrity (Canada National Parks Act, 2000), which includes the traditional practices, like burning and harvesting, of Indigenous people (Woodley, 2010). The archaeological

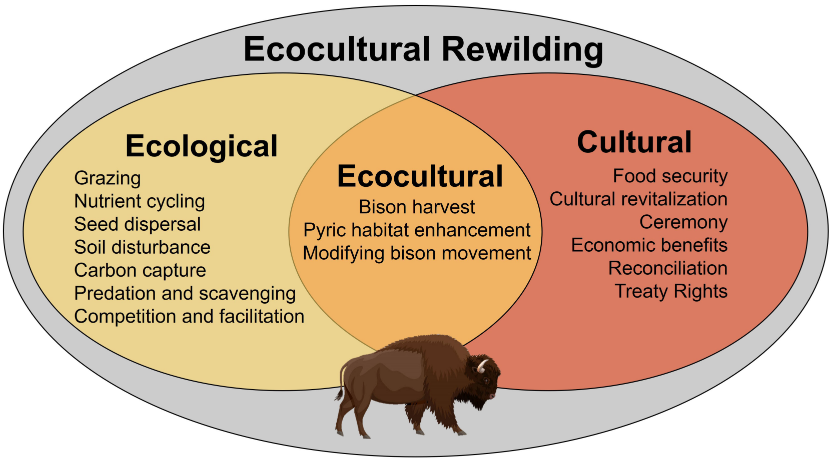

FIGURE 1
Conceptual model of how ecocultural rewilding of North American bison combines the restoration of ecological, cultural, and ecocultural processes.

(Langeman, 2004), historical (Farr and White, 2022), and dendrological (Rogeau et al., 2016) evidence for such practices shaping the ecology of the region is high.

Serious discussions of wild plains bison reintroduction in BNP began when a small, fenced bison herd, which had been a popular tourist roadside attraction for 100 years (Kopjar, 1989), was shut down to restore a wildlife corridor in 1997 (Page et al., 1996). Feasibility studies for wild replacements (White et al., 2001) identified suitable habitat for up to 1,000 wild plains bison inside the park (Steenweg et al., 2016) with a low risk of disease transmission to nearby livestock (Rothenburger and Leighton, 2012). A reintroduction plan soon followed (Parks Canada, 2015b), which emphasized the Indigenous cultural, as well as ecological, benefits.

Such ecocultural emphasis is relatively new in BNP where little consideration has been given to Indigenous cultures since park establishment 134 years BP (Binnema and Niemi, 2006). Modern attempts to correct this are a priority for the Canadian government under the Indigenous Truth and Reconciliation process, which aims to heal and correct the physical and psychological trauma of past colonial practices (National Centre for Truth and Reconciliation, 2020). The restoration of culturally important plains bison populations is an ideal opportunity for government agencies and Indigenous nations to work together, heal relationships, and build trust towards a common goal (Redford et al., 2016; Crosschild et al., 2021; Shamon et al., 2022).

As a case study of an ecocultural rewilding project, we describe the recent reintroduction of bison to BNP within the context of two questions. First, was the bison reintroduction successful from an ecological rewilding perspective? Second, did it appropriately engage Indigenous peoples and restore culturally beneficial practices? We also consider how an ecocultural approach positions the project to meet future challenges, particularly around issues that other bison rewilding efforts inevitably encounter, namely range and population expansion (Sanderson et al., 2008).

2 Context

BNP is within the traditional territories of Treaty 7 Nations, which includes the Siksika, Kainai, and Piikani First Nations of the Blackfoot Confederacy, the Îyârhe Nakoda of the Chiniki, Bearspaw, and Good Stoney First Nations, the Tsuut'ina First Nation, and the Métis Nation of Alberta, Region 3. Ecologically, the area is characterized by a nearly intact pre-colonization baseline (Laliberte and Ripple, 2003) amidst rugged mountains and three ecoregions delineated by elevation (Hebblewhite et al., 2008): montane (1350 – 1500 meters), subalpine (1500 – 2300m), and alpine (2300 – 3600 meters). The montane ecoregion contains the highest-quality ungulate habitat (Hebblewhite et al., 2008) including rough fescue (*Festuca campestris*) meadows, but is largely dominated by lodgepole pine (*Pinus contorta*) conifer forests with patches of Englemann spruce (*Piceae engelmanii*)-willow (*Salix* spp.) and aspen (*Populus tremuloides*). The subalpine ecoregion is primarily Englemann spruce-subalpine fir (*Abies lasiocarpa*)-lodgepole forest, but also contains subalpine grasslands, willow-bog birch (*Betula glandulosa*) shrublands, and avalanche terrain. The alpine region is primarily bare rock and open shrub-forb meadows. The area is characterized by warm summers with short growing seasons, and cold winters with deep snowpacks, except for some steep or windblown terrain.

3 Key rewilding steps

3.1 Scoping for opportunities and constraints (1989-2012)

An early feasibility study identified a unique, globally significant bison rewilding opportunity in BNP (White et al., 2001). Supportive policy, which recognizes bison as protected wildlife, was already in place within but not outside the national park (Canada National Parks Act, 2000). This lack of legal status for bison outside the park presented significant constraints to the project design, but given the ecological and cultural opportunities, they were deemed surmountable (see Section 3.3).

3.2 Stakeholder, indigenous and public consultation (2012-15)

We solicited feedback about potential bison reintroduction at dozens of stakeholder meetings over three years. Feedback was generally positive but with some concerns (Parks Canada, 2014). For example, some ranchers, who hold allotments to graze their cattle on public lands approximately 20 km from the park, had concerns about the low risk of bison transmitting bovine brucellosis or tuberculosis to their livestock. Hunters were concerned about introducing new diseases to wildlife, and the potential for bison to compete with elk and bighorn sheep. Recreationists and horse-riding operators were concerned about public safety and potential property damage. Treaty 7 Nations and the Métis Nation of Alberta were excited by the cultural and ecological benefits, wanted to conduct ceremonies at key phases of the project, and were interested in future employment and bison harvesting opportunities. Environmental groups supported the ecological goals of the project (Figure 1), but worried about long term viability and cost, especially because bison were not considered wildlife if they ventured onto Alberta lands east of the park. Local tourism operators and the overall public welcomed new wildlife viewing opportunities (Parks Canada, 2014; Parks Canada, 2017).

3.3 Building a plan (2015-2016)

In 2015, the Canadian government announced $6.5 million over seven years to rewild bison to BNP, which sent the project into high gear. Feedback from the above consultations guided a reintroduction plan that called for a small number of bison (N=16) to be selected from a disease-free herd and tested extensively after being translocated over the first 5 years (Macbeth, 2016), and for Indigenous blessing ceremonies to occur at all key phases of the project (Parks Canada, 2015b). The plan also included significant mitigations to anchor the bison to a target 1200 km^2 reintroduction zone within the park. This included holding the bison in a soft release pasture for 1.5 years in order for them to calve twice before being released, after which a mix of rugged mountain geography, short sections of wildlife-friendly drift fencing (Laskin et al., 2020), and, when necessary, herding and hazing by staff (Watt and Heuer, 2021) would keep them within the target zone. Some stakeholders had persistent concerns that were eventually overcome by framing the project as a reversible 5-year, pilot where animals would be recaptured and removed if disease was detected or the animals could not be contained within the park (Heuer and Zier-Vogel, 2016).

3.4 Initial ceremony, physical preparations, and the larger Buffalo Treaty (2016)

Indigenous blessing ceremonies helped integrate spiritual perceptions, beliefs, and knowledge from hundreds, if not thousands, of years of coexistence with bison into the rewilding effort. They helped reveal blind spots in the short timeframes normally considered in western science, and brought relevance to the traditional wisdom within Indigenous prayers, stories and songs (Lewis and Sheppard, 2005). The first Indigenous blessing ceremony for the Banff bison rewilding project, held at a road-accessible site near the backcountry reintroduction zone, occurred in September 2016. It acknowledged, celebrated, honored, and spiritually prepared the land for the upcoming return of bison. Hosted by Parks Canada, it was shaped and conducted by elders, knowledge keepers, chiefs, and councilors from the Siksika, Kainai, and Piikani First Nations of the Blackfoot Confederacy, and the Îyârhe Nakoda of the Chiniki, Bearspaw, and Good Stoney First Nations.

Parks Canada also undertook physical preparations in anticipation of bison arriving in the reintroduction zone. These included designing and building several wildlife-friendly bison drift fences to augment the rugged mountain topography on the perimeter of the target reintroduction zone (Laskin et al., 2020), prescribed burning of meadows to improve habitat quality (Parks Canada, 2015a), and building of the 16 ha soft release pasture in the backcountry (Parks Canada, 2016).

An Indigenous-led Buffalo Treaty (Crosschild et al., 2021), now signed by over 40 Indigenous nations, also took form at this time.[1] Its purpose is to "recognize buffalo as a wild free-ranging animal and as an important part of the ecological system; to provide a safe space and environment across their historic homelands, on both sides of the United States and the Canadian border, so together the buffalo can lead First Nations to nurture their land, plants and other animals and once again realize the buffalo ways for future generations". Larger in scope than the Banff bison rewilding project alone, it nonetheless features Banff as an inspiring example of what can be done, and advocates for its continued success. One of the first resolutions of its signatories, for example, was a formal request to the Alberta government to recognize plains bison as wildlife in 2016[2].

3.5 Transfer of bison from Treaty 6 to Treaty 7 lands (2017)

A second Indigenous ceremony acknowledged the transfer of animals from the traditional territories of Treaty 6 Nations (in and around Elk Island National Park, Alberta) to Treaty 7 and Metis Area 3 nations, whose traditional territories include parts of BNP. This included pipe ceremonies and speeches from Indigenous leaders of the Enoch Cree, Ermineskin Cree, O'Chiese, Samson and Sunchild (Treaty 6 nations) and the Siksika, Kainai, and Piikani First Nations of the Blackfoot Confederacy, and the Îyârhe Nakoda of the Chiniki, Bearspaw, and Good Stoney First Nation (Treaty 7 nations). It also featured Indigenous drumming, singing, and dancing within a few hundred meters of the soon-to-be-transferred bison.

The bison destined for Banff were captured, seperated and tested over the previous weeks. Sixteen animals were selected from the ~400 animals in the Elk Island herd, known for its relative genetic purity and lack of bovine brucellosis and tuberculosis (Markewicz, 2017; Figure 2). We selected for animals of young age (2-3 years), 10 females and 6 males, pregnancy (all females confirmed pregnant through rectal palpation), health (Macbeth, 2016), and rare alleles and unrelatedness (Wilson et al., 2023). Animals were baited and handled within Elk Island's chute and pen system as per Parks Canada's approved animal welfare protocols during a roundup to remove excess animals from Elk Island's fenced population every two years (Markewicz, 2017). All animals slated for the BNP reintroduction were tested for diseases of concern by Canadian Food Inspection Agency and Parks Canada veterinarians, then held in a 2-ha. pen for a two-week quarantine period where they were acclimated to hay and limited human presence.

The Indigenous transfer ceremony coincided with the end of the quarantine period on January 30, 2017. The next day, the 16 animals were herded through Elk Island's chute and squeeze system one last time so they could be drenched with a deworming compound (Ivermectin^{TM}) and injected with a long-acting tranquilizer (0.3 mg/kg of Zuclopenthixol acetate) (Pohlin et al., 2019; Slater et al., 2021) and fitted with 3.8-5cm diameter rubber tubes over their horns to minimize injury to crate mates on the upcoming journey. They were then loaded in groups of three (males) or four (females) each into five standard ten-foot (2.98m-long by 2.43m-wide by 2.92m-high) metal shipping containers (Sea-Containers Ltd). These had been retrofitted with 0.01m^2 hatches cut into the roof for additional drug administration, by jabstick, if needed, and 0.45m-high by 1.5m-long ventilation openings cut into the top side walls. Side and back walls were reinforced with 2cm-thick by 2.4m-high plywood sheets, and anti-slip 1cm-thick rubber mats from horse trailers were

1 https://www.buffalotreaty.com/

2 https://static1.squarespace.com/static/5e5fe077316ef31fa3aa0210/t/5e67227bb2fd91655fc3c4bf/1583817340118/2016+Buffalo+Treaty+Alberta+Wildlife+Bison+letter+and+resolution+signed.pdf

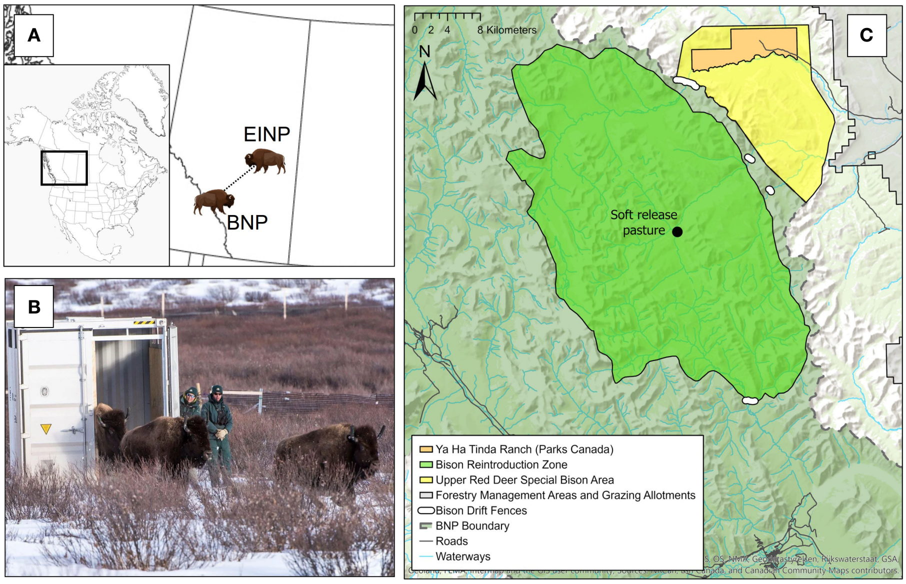

FIGURE 2
The 2017 reintroduction of Plains bison to Banff National Park (BNP). Sixteen bison were transferred from Elk Island National Park (EINP) to BNP **(A)**, released into a soft-release pasture and held for 18 months **(B)**, then released into the 1200 km^2 core reintroduction zone **(C)**.

borrowed to use on the floors. The containers were strapped and secured to five waiting 1-ton flatbed trucks, where the bison were loaded using the ramp of Elk Island's chute system.

The loaded trucks were driven 400 km from 5pm to 12am in -20° C temperatures (Figure 2). A single visual check was made at the halfway point of the journey using a ladder and headlamp; all animals were well settled, with half standing and half bedded. This settled behavior persisted to the end of the road journey and for the remainder of the night while the trucks sat parked at the end of a gravel road within 20km of the reintroduction zone. A Kamov KA-32 helicopter with a lifting capacity of 4,500 kg arrived at daybreak, and, using a 30m longline, slung each of the loaded containers ~25 km over the final mountain ridge to the soft release pasture in the center of the backcountry reintroduction zone. Containers were attached to the long line by way of a swivel hook and a 4-point cable harness which connected to the top corner pockets of the metal shipping containers. A 2m-diameter drogue chute, tied to a bottom corner of each container, minimized spin during flight, and two 3m ropes tied to two other bottom corners helped ground crews orient containers upon landing. This aerial lift system was tested the day prior to animal translocation using an identical container filled with a volume of hay and compressed feed to approximate the weight of 4 bison.

3.6 Bison soft release pasture (2017-18)

All 16 animals emerged into the soft release pasture with only minor skin abrasions and fed on hay and drank from water troughs within an hour (Figure 2). Only 2 bison exhibited ataxia, presumably from the long-acting tranquilizer. They moved normally within 10 minutes of exiting the containers.

Animals were held in the soft release pasture for the next 18 months where they calved twice, which bison ranchers advise is important when anchoring animals to a new location (Kremeniuk, 2016). Each female gave birth to their first calf 3-4 months after translocation, sired by bulls in Elk Island the previous summer, which added significant genetic variation to the founder herd (Wilson et al., 2023). All 10 females then bred with one of the 6 translocated bulls while still in the soft release pasture the following summer (2017) and gave birth to a second crop of calves, which were mostly born before all the animals were released in July 2018.

The location of the 18-ha soft release pasture was of moderate bison habitat quality (Steenweg et al., 2016; Keery, 2019) and was selected due to its central location in the target reintroduction zone and the presence of existing infrastructure (a Parks Canada backcountry patrol cabin, fenced horse pasture and corral and tack shed; Figure 2). These were temporarily retrofitted to meet the needs of the project. For example, the 6-ha horse pasture was converted to the main bison paddock, where the animals were fed hay and compressed alfalfa cubes for most of the year, and a larger (12ha) summer pasture was constructed beside it, where the animals grazed on natural vegetation in the summers and were exposed to steep slopes, burned forest, and a river. Both pastures were enclosed with 2.4m-high knotted page-wire game fence (Tree Island Steel) with a 30cm band of plastic snow fencing attached at bison-eye-height (~1m) for visibility. The page-wire was stapled to 2X4 dimensional lumber screwed to the 1.2m-high pressure treated posts that were already dug around the perimeter of the old horse pasture (4m spacings), augmented by 3.6m-high, 7.3cm diameter metal posts sunk 1.2m into the ground to brace gate openings and corners. The summer pasture was similarly fenced, but with 2.8m-long metal T-posts driven 40 cm into the ground in lieu of the preexisting wooden posts, and black windscreen tarps and plywood slats suspended across the Panther River on adjustable 5mm cables at two locations. All fence components were slung in by helicopter and constructed, by hand, by park staff, volunteers and local contractors (Parks Canada, 2016).

Once the bison were translocated, one to two Parks Canada staff at a time worked 9-day shifts for the 544-day soft release period (Feb 2017 to July 2018). Access and egress normally required two days travel by horseback or ski. Duties at the pasture included feeding bison hay and alfalfa cubes, pumping water into troughs, shoveling and stockpiling manure, and recording bison health observations.

Adult bison consumed an average of 0.3 square bales of hay per day per individual (9 kg), which increased to 0.6 bales/day/individual (18 kg) when the 10 females nursed calves. An additional 1.14 - 2.7 kg of alfalfa cubes were fed and consumed per bison per day. Drinking water was pumped from the river directly into troughs in summer or transported via slip tank and snowmobile in winter and pumped into propane-heated troughs. Water consumption for the entire herd was 300 liters per day for 16 animals at the beginning of the soft release period, and grew with the number of animals, to a maximum of 470 liters a day for 31 animals just before they were released.

We fed minerals via 2 horse/cattle salt blocks (Windsor Salt Ltd.) which contained granulated salt, zinc, iron, manganese, copper, iodine, cobalt, and selenium. We also provided a similar loose mixture in two nearby wood bunkers to avoid aggressive interactions due to competition.

Animals were fed chopped hay from wooden bunkers for several days before release, into which a deworming crumble (Safeguard™) was distributed and consumed. This was a follow up to the deworming drench applied while the animals were still at Elk Island. Feces were tested 7 days after both treatment and negligible amounts of common parasites, such as Eimeria, were detected after both treatments, with no other significant parasites. This may have been partially due to significant efforts to remove manure from feeding and bedding areas every day while the animals were in the soft release pasture: an average of 16 kg of manure per animal per day was shoveled and stockpiled for each of the 544 days.

3.7 Creating an indigenous advisory circle (2018)

With the release date of the bison fast approaching, the need for a forum where Indigenous nations could advise Parks Canada on the management of wild bison became apparent. This led to the establishment of the BNP Indigenous Advisory Circle (Parks Canada, 2019). Inspired by the reintroduction of bison, its scope quickly grew to cover all park management issues. The inaugural meeting in May 2018 was a milestone in Parks Canada's reconciliation journey; it marked the first time Indigenous groups had a voice in how the park was managed since it was established 133 years before.

3.8 Releasing the bison (2018)

A third Indigenous ceremony was held days before the final release of the bison at the remote soft release pasture in late July 2018. Twelve chiefs, elders, knowledge keepers, councilors, and consultation staff, representing all Treaty 7 nations (the Siksika, Kainai, and Piikani First Nations of the Blackfoot Confederacy, the Îyârhe Nakoda of the Chiniki, Bearspaw, and Good Stoney First Nations, the Tsuut'ina First Nation, and the Métis Nation of Alberta, Region 3) were flown in by Bell 212 helicopter to conduct ceremonies at the backcountry site where bison were soon to be released.

Three days later, on July 29, 2018, the fence was cut, and the herd (which had almost doubled to 31 animals over 2 calving seasons) was released. Remote camera imagery shows the animals found the opening 8 hours later and exited in the middle of the night. A 300m-long trail of manure roughly bounded by piles of dead wood proved fruitless in guiding them to the nearest meadow system: as soon as they reached the end of it, the animals turned sharply into thick forest, traversed a steep canyon, and climbed above tree line, settling in a high subalpine basin 6 km from the release site, where they remained for the next 1.5 months. Such elevational migrations became common for the bison over the next 3 summerss (Zier-Vogel and Heuer, 2022). Although it is normal for native mountain grazers to move upwards to access palatable and nutritious vegetation as it emerges from the melting snow (Hebblewhite et al., 2008), the speed at which the bison – which were just translocated from the flatlands of Elk Island- adapted to their new mountain environment was remarkable.

3.9 Wide-ranging bison prompt small changes to transboundary policy

Most of the herd remained within the target reintroduction zone that first month except for two separate bulls, which wandered outside the park. One was recaptured and the other destroyed within a few days, but both were lost to the project. This prompted the Government of Alberta to establish the 240 km^2 Upper Red Deer Special Bison Zone adjacent to the park, which protects bison in a small corner of the province of Alberta until Parks Canada can redirect them back into the park. [3] This was driven by a concern that the rest of the herd might follow the wandering bulls, which did not happen, largely because of mitigations like drift fences and herding, which work better for larger and less obstinate groups of female bison with young. Drift fences prevented bison from leaving the park 57 times over the first three years (Laskin et al., 2020; Zier-Vogel and Heuer, 2022), while herding them away from boundary areas worked on all 7 occasions it was tried (Laskin et al., 2020; Watt and Heuer, 2021; Zier-Vogel and Heuer, 2022).

Recent (2021) changes to provincial policy, which now recognizes Wood bison (*Bison bison athabascea*) as wildlife in discrete areas of northern Alberta, provide a model for how plains bison might be accommodated outside the park in Banff but have yet to be realized[4].

3 https://open.alberta.ca/publications/upper-red-deer-river-special-bison-area

4 https://www.alberta.ca/wood-bison-regulation

3.10 Ecological and cultural monitoring point toward a transboundary future (2018-2023)

Most of the research and monitoring of the bison centered around location data from GPS collars fitted to 5-10% of the population via chemical immobilization from horseback over 5 years (Vectronics Aerospace Inc.). Collar data shows bison movements have stabilized since the animals were released in 2017 (Zier-Vogel and Heuer, 2022) but visits to boundaries of the target reintroduction zone persist, mostly in a northeast direction (Figure 3B). Drift fencing (Figures 4B, C) and herding (Figure 3A) has helped contain such extralimital movements (with the exception of a few bulls – Figure 4A) but habitat and movement modelling suggests such exploration will continue (Hebblewhite, 2016; Verzuh and Merkle, 2022). This is more likely given the herd's rapid growth (Figure 3C – 38% per year), presumably because the animals are accessing a high-nutrition diet, especially in summer (Verzuh and Merkle, 2022) and have experienced low mortality (Parks Canada, 2022). Only two bison calves are known to have been lost in the young herd so far, likely due to wolf predation.

Despite high growth of bison numbers, qualitative rangeland health assessments have not identified overgrazed areas in BNP so far, with bison having only accessed a small portion of the available forage. Evidence for bison spatiotemporal home range overlap with GPS-collared elk or bighorn sheep is minimal, although resource selection analyses have revealed shared habitat preferences that suggest competition may occur if bison densities increase (Martin and Hebblewhite, 2022; White, 2022).

A cultural monitoring survey of the BNP bison was completed in 2020 (Stoney Nakoda Nations, 2022). The first biocultural study of its kind in BNP, it consisted of Indigenous technicians interviewing elders in advance of riding, by horseback, through the bison area for 5 days (Figure 5) and reporting back to elders with photos and videos. It differed in approach from western methods but arrived at some similar recommendations. In addition to future Indigenous harvesting of bison, it called for the animal to be considered as wildlife outside the park, and greater interjurisdictional cooperation for its future management (Stoney Nakoda Nations, 2022).

3.11 Future challenges

Unsurprisingly, and like most other free ranging bison populations (Sanderson et al., 2008), managing herd growth and expansion of the Banff bison will be central issues in the management of this newly rewilded population in the near future (Parks Canada, 2022). Ironically, the technical mitigations that contributed to the success of the rewilding project in its initial years (e.g., collaring and monitoring many animals, constructing and maintaining drift fences in remote areas, herding animals on short notice when necessary) are now becoming logistically and financially challenging to maintain as the herd grows and expands. Policy changes that accommodate bison onto adjacent Alberta public lands would help ease these challenges, not only by reducing the need to contain them to a smaller area, but also for how it provides some road access to bison, which would facilitate

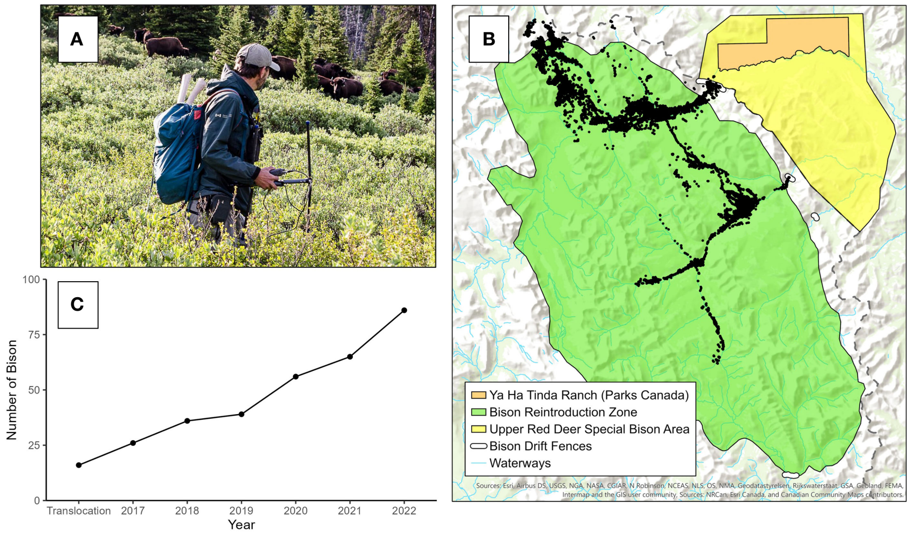

FIGURE 3
Ecological monitoring of bison following their 2017 reintroduction to Banff National Park integrates various forms of data collection including remote camera observations, radiotelemetry **(A)**, and GPS collared bison **(B)** to assess body condition, behaviour, herd demographics, and population numbers **(C)**.

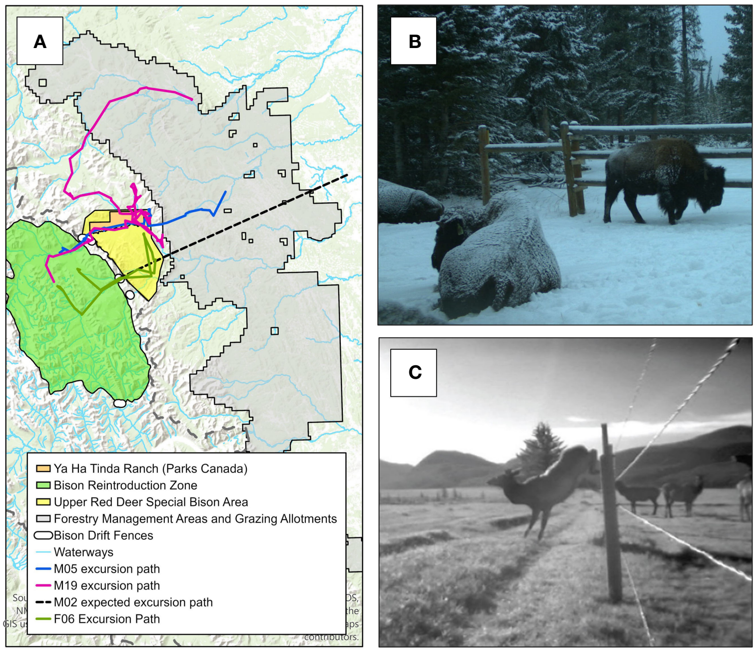

FIGURE 4
Bison excursions from the core reintroduction zone from 2017 to 2023 **(A)**. Drift fences were largely effective at preventing excursions **(B)** while allowing other wildlife species like elk (*Cervus canadensis*) to pass through **(C)**.

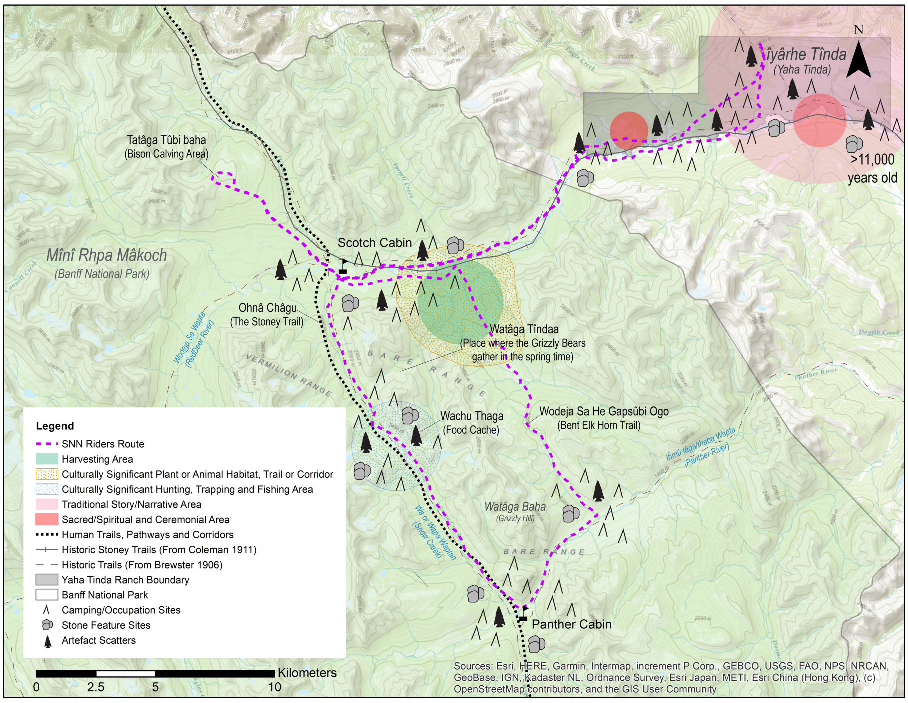

FIGURE 5
Map from Stoney Nakoda Nations (2022) of culturally important areas identified during the bison cultural monitoring. Stoney Nakoda wove together western science and traditional knowledge with a cultural monitoring process that used ceremony, elder interviews, fieldwork, and elder reconnection. The full cultural monitoring report is available online.

Indigenous and non-indigenous hunting as a means of regulating herd size. Such access issues are significant given the remoteness of the area and the size of a bison carcass (up to 1,000 kgs). Managing for a population of just 200 bison at today's growth rates, for example, would require removing 40-50 animals per year.

4 Discussion

The ecocultural rewilding of plains bison to Banff National Park has been an ecological and cultural success. Ecologically, we have reintroduced only the 5th free roaming population in the world of a red-listed species, and, after 5 years, the animals are healthy, growing rapidly and, except for a few wandering bulls, are anchored to the target reintroduction zone (Zier-Vogel and Heuer, 2022).

Culturally, the incorporation of Indigenous ceremony and traditional knowledge, and the establishment of an Indigenous Advisory Circle, have engaged Indigenous peoples in a project that has not only rewilded a species, but restored a cornerstone of endangered plains cultures. This has empowered and inspired many other bison restoration efforts, and has brought relevance to ancient Indigenous prayers, stories, and songs for a new a new generation of Indigenous people (Crosschild et al., 2021).

The strength of the ecocultural approach is only building for the Banff bison rewilding project. After ten years of working together, a trust has developed between Parks Canada and Indigenous nations that is about to deepen as the ultimate plains cultural practice – harvesting of bison by Indigenous people – becomes a fundamental ecological tool for managing the size and range of the growing herd. Discussions are underway to determine how and where this will unfold, and focusing new attention on the interjurisdictional inconsistencies in bison policies that hamper progress. Interestingly, the ecocultural approach is framing the rewilding of Banff bison as much more than an ecological issue of saving a red-listed species; with Indigenous harvest imminent, it has become an issue of human rights.

The additional pressure this focusses on resolving policy differences between jurisdictions would not have happened had the project been framed as only an ecological rewilding effort. Plains bison have been hunted by humans for millennia and the restoration of this relationship is as important as restoring the animal itself (Farr and White, 2022; Shamon et al., 2022) and helped us overcome the oversight of not including people in our rewilding effort (Jørgensen, 2015). Doing so not only broadened our initial success beyond ecological to cultural restoration, but also created a more resilient and diverse foundation from which we have more tools and voices to meet future challenges. The ecocultural approach has become our collective strength.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by Parks Canada Animal Care Task Force. The study was conducted in accordance with the local legislation and institutional requirements. Written informed consent was obtained from the individual(s) for the publication of any identifiable images or data included in this article.

Author contributions

KH: Methodology, Project administration, Writing – original draft, Conceptualization. JF: Conceptualization, Visualization, Writing – review & editing. LL: Writing – review & editing. MH: Conceptualization.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The role of social and political factors in the success of rewilding projects

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The ecological aspects behind the success and failure of rewilding projects have been looked at in literature and case studies, but rarely have sociopolitical factors been included in these classifications. To truly determine which factors lead to success in rewilding projects, inclusive of sociopolitical factors, we created global models that analyze 120 case studies from IUCN's "Global Re-introduction Perspectives" that fit under IUCN's definition of rewilding. Models included the ten guiding principles for rewilding from IUCN's Rewilding Thematic Group, success factors, and threats to success as defined from existing literature. We measured the self-reported "level of success" from the case report examples against the guiding principles, success factors and threats to determine which were more likely to be associated with successful rewilding projects. Local awareness of the benefits of rewilding and illustrating a proof of concept of rewilding were the factors that were most strongly associated with higher levels of success in rewilding projects, as self-reported by case report authors, as well as Guiding Principle 9 "rewilding recognizes the intrinsic value of all species". Our results indicate that both ecological and sociopolitical factors are critical to successful rewilding projects and both need to be accounted for and included in future planning of rewilding projects to maximize the possibility of successful rewilding.

KEYWORDS

rewilding, reintroduction, conservation translocation, social science, success, policy, human-wildlife conflict

1 Introduction

Rewilding is defined by the International Union for the Conservation of Nature (IUCN) as "the process of rebuilding, following major human disturbance, a natural ecosystem by restoring natural processes and the complete or near complete food web at all trophic levels as a self-sustaining and resilient ecosystem with biota that would have been present had the disturbance not occurred…" (Carver et al., 2021). One of the activities that falls under the umbrella of rewilding, if done with the intention of restoring natural processes to a landscape, is reintroducing "lost" species (native species that were formerly present in a landscape but have been extirpated by humans) (Lipsey et al., 2007; Brown et al., 2011; Seddon et al., 2014; Andrews et al., 2022). For the purposes of this paper, we focus specifically on rewilding through species reintroduction, as opposed to any of the other methods of rewilding that include activities like passive land abandonment, island taxon replacement, etc. Rewilding through reintroduction intends to recreate ecologically appropriate trophic interactions that have been missing since their extirpation (Sandom et al., 2020). Despite the great promise of restoring natural ecosystem processes rewilding projects do not always succeed. The ecological aspects behind the success and failure of rewilding projects have been thoroughly assessed (Torres et al., 2018). However the sociopolitical factors associated with rewilding, which have strong implications for the success or failure of rewilding projects (Estrada, 2014; Lorimer et al., 2015; Coz and Young, 2020), are often overlooked.

Rewilding has an inherently ecological focus, which is reflected in the literature, however rewilding also affects human social and political issues which can ultimately influence whether rewilding activities succeed or fail (Pettorelli et al., 2018; Wolf and Ripple, 2018; Martin et al., 2021). The most recent definition from IUCN's Rewilding Thematic Group, used above, includes human and societal factors, such as looking at local engagement and support and the perceived intrinsic value of wildlife (Carver et al., 2021). When looking at rewilding in practice and outside of academic literature, these factors appear frequently in case reports (Soorae, 2008; Soorae, 2010; Soorae, 2011; Soorae, 2013; Soorae, 2016; Soorae, 2018; Torres et al. 2018; Sandom and Wynne-Jones, 2019; Soorae, 2021; Underwood et al., 2022), but they have not made it into the scientific literature. It is clear that social and political factors, such as human wildlife conflict, have effects on the success of rewilding projects, yet they are seldom measured in comparison to ecological indicators of success (Pettorelli et al., 2018; Vasile, 2018; Sandom et al., 2019; Coz & Young, 2020). For example, Torres et al. (2018) was the first to establish a set of indicators to measure rewilding progress but did not include any social or political indicators. The authors instead looked specifically at the level of human management of the landscape, and amount of ecological integrity in rewilded systems as indicators of success – leaving out social and political enabling conditions and their potential to influence project outcomes.

Despite potentially providing benefits for people and nature, public opposition around the potential for human-wildlife conflict, as well as other cultural and social issues, has caused many rewilding projects to fail if those issues are not resolved (Lorimer et al., 2015; van der Zanden et al., 2018; Martin et al., 2021). While physical damage caused by wildlife is usually cited as the main reason for conflict (Carver, 2017; Bavin et al., 2020, p. 201; Coz and Young, 2020), oftentimes there is significant conflict between people and wildlife that remains even if the physical damage has been reduced or eliminated. In addition to conflicts between people and wildlife, there are often conflicts between people (human-human conflict) that cause a project to fail. For example, in Norway, farmers suspected that 'naturally recolonizing' wolves were actually secretly bred and reintroduced (Dickman, 2010). In this case, farmers blamed external agencies for imposing wildlife and the risks associated with wildlife upon them – a trust human-human conflict (Dickman, 2010). Such conflicts between people also extend to anticipated conflict from animals if rewilding does occur. The likelihood of perceived [or anticipations of] conflict is particularly high if the species has been absent from a landscape for hundreds of years, which increases the potential to impede rewilding projects' progress because conflicts do not yet exist and must be anticipated (Auster et al., 2020). If not properly addressed human-wildlife conflict and other problems between people and wildlife, as well as between people, can ultimately diminish the benefits that rewilding can provide.

Media portrayals of Eurasian beaver (*Castor fiber*) rewilding in Europe (Kaphegyi et al., 2015), and grey wolf (*Canis lupis*) rewilding in Colorado (Niemiec et al., 2020) have focused mainly on reporting conflicts between people and the named species, and the potential for more conflict should the natural range of the species expand – a major goal of rewilding. The focus on conflicts in mainstream media has caused public perceptions of the rewilding of these species to become increasingly negative, perpetuating concerns over the potential loss of livelihoods, and threats to safety, should these species return to the landscape c. Thus, arguments for rewilding need to be articulated clearly enough to prevent conflict from occurring.

Building on Torres et al. (2018) indicators of ecological success for rewilding projects, Segar et al. (2022) developed a set of key success factors and threats to success that include both ecological and social attributes. Segar et al. (2022) conducted a mixed methods approach of utilizing ecological indicators from Torres et al. (2018), and social and political attributes, which highlighted that there are also social and political threats and success factors involved in rewilding. However, Segar et al. (2022) only analyzed case examples from Europe, which leaves out key areas where rewilding occurs globally and potentially limits the number of success factors and threats identified through the process.

In this paper, we test the success factors and threats identified by Segar et al. (2022), and IUCN's ten global "Guiding principles" (Table 1) – a suite of ten principles meant to guide rewilding projects towards success (Carver et al., 2021) – against a set of success metrics and threats to rewilding success, as defined by the authors of rewilding reports, that include social, political, and ecological factors. We analyze data from known rewilding case studies against the Guiding Principles for Rewilding, as well as identified sociopolitical success factors and threats, and ask the following research questions:

1. Are there common sociopolitical success factors and threats (Segar et al., 2022) that determine the level of success of a rewilding project?
2. Does implementing each "guiding principle for rewilding" affect the level of success of a project differently?

We predict that:

1. The sociopolitical factors of human-wildlife conflict and mitigation are the primary sociopolitical factors that affect

TABLE 1 Guiding Principles for Rewilding (Carver et al., 2021).

Principle	Definition	Principle Shown in Practice
Principle 1 – Restored food webs	Rewilding uses wildlife to restore food webs and food chains.	Reintroducing a species to create a trophic cascade in an ecosystem, leading to enhanced ecosystem function through regulation of food chain.
Principle 2 - Connectivity	Rewilding plans should identify core rewilded areas, ways to connect them, and ensure outcomes are to the mutual benefit of people and nature.	By connecting isolated areas, wildlife corridors can help to enhance biodiversity and animal populations of rewilded species.
Principle 3 - Recovery	Rewilding focuses on the recovery of ecological processes, interactions and conditions based on similar healthy ecosystems.	Rewilding should aim to restore self-sustaining and resilient ecosystems, using an appropriate ecological reference point.
Principle 4 – Dynamic ecosystems	Rewilding recognizes that ecosystems are dynamic and constantly changing.	Recognizing that temporal cange, but exernal and internal, is a fundamental attribute of ecosystems and the evolutionary processes critical to ecosystem function.
Principle 5 – Climate change	Rewilding should anticipate the effects of climate change and act as a tool to mitigate its impacts.	Rewilding projects have medium- to long-term time scales that span the predicted scales and magnitures of global climate change. It is also considered a nature-based solution (NbS) to climate change.
Principle 6 – Local engagement	Rewilding requires local engagement and community support.	Rewilding should be inclusive of all stakeholders and embrace participatory approaches and transparent local consultation in the planning process for any project.
Principle 7 – Science	Rewilding is informed by science and considers local knowledge.	Traditional ecological knowledge (TEK) provides a complementary body of knowledge to science and collaborations between researchers.
Principle 8 - Adaptability	Rewilding is adaptive and dependent on monitoring and feedback.	Monitoring is essential to provide evidence of short-term and medium-term results with long-term rewilding goals in mind, required to determine whether trajectories are working as planned
Principle 9 – Intrinsic value	Rewilding recognizes the intrinsic value of all species.	Humanity has an ethical responsibility to both respect and protect the value that species and ecosystems have outside of just the goods and services that they provide to humans
Principle 10 – Paradigm shift	Rewilding is a paradigm shift in the coexistence of humans and nature.	Rewilding should create a greater awareness of global ecosystems that are essential to life on the planet, shifting advocacy and activism for change in political will and to help shift ecolofical baselines toward recovering full functioning trophic ecosystems – less overexploitation of nature

the level of success of a rewilding project. (Dickman, 2010; Kaphegyi et al., 2015; Niemiec et al., 2020).

2. A combination of both ecological and sociopolitical guiding principles are important in determining the success of a rewilding project due to their numerous appearances in both peer-reviewed literature and case examples on rewilding (Torres et al. (2018); Segar et al., 2022).

2 Materials and methods

The IUCN Commission for Ecosystem Management (CEM) Rewilding Thematic Group (RTG) drafted a set of ten “Guiding Principles for Rewilding” (Carver et al., 2021) with the aim of improving the effectiveness of rewilding as an intervention to achieve global targets such as the UN Decade on Restoration goals. Here we assess these 10 guiding principles as indicators of success in rewilding projects. We used a global set of case studies from IUCN’s “Global Re-introduction Perspectives” (later “Global Conservation Translocation Perspectives”), hereby known as “Global Perspectives” from 2008-2021 (Soorae, 2008; Soorae, 2010; Soorae, 2011; Soorae, 2013; Soorae, 2016; Soorae, 2018; Soorae, 2021) against “Guiding Principles for Rewilding”, success factors and threats. While most of the “Global Perspectives” case studies were drafted before the publication of “Guiding Principles for Rewilding”, We compared and contrasted the “Global Perspectives” case studies and the “Guiding Principles for Rewilding” against one another to validate the applicability of the principles to a set of global case studies, as they are two IUCN-vetted pieces of literature. We compared each of the 10 Guiding Principles for Rewilding (see Table 1) to the known factors that are associated with success and threats to success (see Table 2) to analyze whether or not the principles were relevant in determining the success of rewilding projects.

2.1 Global perspectives case reports

Of the hundreds of case reports during the span of 13 years, from IUCN’s “Global Perspectives”, we identified 120 cases that counted as “rewilding” according to IUCN definition from the RTG (Carver et al., 2021), namely that the reintroduction projects that we selected were chosen due to their overall goal of restoring ecosystem function through species reintroduction, rather than a project that was designed solely for the purpose of conserving the species in question. While this may be subjective in nature due to our application of the definition to these projects and its high-level nature, we believe that these case studies do fit the requirements for a rewilding project. We acknowledge that our interpretation of the definition may have excluded certain cases that may include elements of rewilding. All selected case reports were in the categories “reintroduction” or “conservation translocation”. We

TABLE 2 Rewilding success factors and threats to success that were identified and used by Segar et al. (2022) in a sample of European rewilding case studies.

Factor	Threat or success	Definitions and activities
Awareness	Success	Rewilding concept appeal
		Strong stakeholder collaboration
		Positive local perception of site
Nature-based economy	Success	Local engagement and pride
		Sustainable funding sources
Proof of concept	Success	Showcasing intermediary results
		Pilot studies demonstrating rewilding potential
Species management	Success	Keystone species reintroduction
		Human-wildlife conflict mitigation
Human-wildlife Conflict (HWC)	Threat	Poaching
		Species persecution
Law and Policy	Threat	Development policies
		Common Agricultural Policies
Land and Water Management	Threat	Hunting
		Over-grazing
		Over-fishing
		Drainage and river regulation
Land-use Change	Threat	Agricultural expansion
		Habitat loss and fragmentation
		Encroaching urbanization
		Road infrastructure
Pollution	Threat	Water pollution
Biotic Pressures	Threat	Invasive species
		Inbreeding depression

only included terrestrial vertebrate species in our analysis, as these species tend to have higher amounts of conflict than terrestrial invertebrates (Torres et al. 2018). Marine environments face unique threats and social and political issues not present in terrestrial environments, and thus are outside of the scope of this paper.

From each case reports we gathered information that describes the social and/or political factors that are related to project success (see Table 2). The success or failure of a project was self-determined by the author of each case report and were assigned the following rating: failure, partially successful, successful, and highly successful (Soorae, 2008; Soorae, 2010; Soorae, 2011; Soorae, 2013; Soorae, 2016; Soorae, 2018; Soorae, 2021). We then tested the association between these four self-assessed ratings of success or failure against the factors and threats that are known to be associated with project success as described by Segar et al. (2022): 1) success indicators; 2) reasons for the level of success; 3) difficulties faced during the project; and 4) project name. Of the six categories of threats to success only two were related to sociopolitical threats and of the nine factors related to success of a project six were sociopolitical in nature (Table 2).

2.2 International Conservation of Nature guiding principles for rewilding

The RTG's principles were developed through a combination of 1) a literature review to establish the drivers behind the evolution of rewilding and inform questions for the rewilding pioneers survey; 2) a rewilding pioneers survey, which included 25 questions relating to historical and current rewilding concepts and practice sent to selected rewilding experts identified through publications in the literature review, published books, and by personal recommendations; and 3) a series of five workshops to solicit expert opinions from more than 100 experts from geographically diverse locations (Carver et al., 2021). The "Guiding principles" are meant to both clarify the concept of rewilding and improve its effectiveness as a tool to achieve global conservation targets, such as the U.N. Decade on Ecosystem Restoration (Carver et al., 2021). As these principles are meant to serve practitioners, meet global goals, and have been created through a comprehensive methodology, we consider them as criteria for success in rewilding projects. To identify which of these principles, when employed, may predict success we analyzed them against the IUCN "Global Perspectives," self-reported levels of success. Of these principles, four relate to social or political themes (see Table 1 for the principles and their definitions).

In this analysis, we first described the species, class, continent, and year of the case report, and then assessing each case report for the presence of each guiding principle. Each success level was coded between "0" and "4", with no data = "0", failure = "1", partially successful = "2", successful = "3", and highly successful = "4". The existence of the principle was coded as a "1" and the non-existence of the principle was coded as a "0" (see Supplemental Online Material (SOM) Table 2 for all coded case studies). Each case study author was asked to assess the level of success of their project, subjectively, based on the success indicators that they chose. All levels of success were pre-determined by the authors of each case study, and therefore the numbers of 0-4 were just allocated during the coding process according to the level of success described by that author. While this may limit the objectivity of the levels of success across all case studies, as each case study chose their own success indicators to measure against, these were the only levels of success available to us to use when assessing each case study.

2.3 Rewilding success factors and threats to rewilding success

Utilizing the same framework as above when assigning codes to case studies, we looked at success factors and threats within the "Guiding Principles", assigning "1" for the existence of a threat or success factor, and a "0" for the non-existence of a threat or success factor" for any particular case report (see Supplemental Online Material (SOM) Table 2 for a list of all case reports included and the existence or absence of success factors and threats to each case report). We also used rewilding success factors and threats to rewilding success (Table 2) from Segar et al. (2022) to diversify the criteria for determinants of success (Table 2) that are in our analysis, in addition to looking solely at guiding principles as determinants of success. These combined are a new framework for analyzing key success factors of and threats to rewilding globally. Where IUCN's RTG took a global approach to determine overarching principles, Segar et al. (2022) looked specifically at seven European sites to determine success factors and threats to rewilding (Table 2), thus we assessed and expanded Segar et al. (2022) success factors and threats to success globally. While the factors used by Segar et al. (2022) are rooted in specific case studies from Europe, the context of these factors is broad enough that they should be applicable to rewilding projects anywhere in the world. Obviously they would not include any site specific issues (e.g. species or habitat specific), but the Segar et al. (2022) factors remain the best published data and assessment of rewilding, thus are an important component of our analysis.

2.4 Analysis

To address question 1, *what are the sociopolitical factors associated with rewilding success*, we used the list of factors thought to be threats to success and associated with success of rewilding projects as defined by Segar et al. (2022) (Table 2) as the predictor variables. The response variable was the defined level of success of a project. To address question 2, *do the guiding principles affect rewilding success*, the 10 guiding principles were the predictor variables and the defined level of success of a project was the response variable. We coded each case report according to species, class, continent, year, success level, success factors and threats from Segar et al. (2022), as described above, and if they exhibited any of the Guiding Principles for Rewilding (All models are shown in SOM Table 2). Based on the reading of each of the included case reports we determined which Guiding Principles (Table 1) and which factors that are considered threats or associated with success of rewilding projects (Table 2) were associated with each case report.

To address each question we created *a priori* linear regression models, using R version 4.2.2 and the lme4 package to assess the association of guiding principles and/or factors that are thought to be threats or associated with the success of rewilding projects as predictors of the defined levels of success of each case report. We also formulated null models, which assumed no control for taxonomic class, year of the rewilding or continent, for comparison with each of the *a priori* models. All models were formatted as generalized linear mixed models in the Gaussian family with an identity link. *A priori* models had random effects of year, taxonomic class, and continent since different case reports included different case studies of the same species in different continents over different years that produced different success levels. Finally, we combined the different *a priori* models into one global model to compare threats, success factors, and guiding principles against class, continent, and year. Models were ranked based on Kullback- Leibler information (Burnham and Anderson, 2004; Roberts and Luther, 2023).

Support for each model was analyzed with Akaike's Information Criterion corrected for small sample size (AIC_c). We also assessed the model weight (w_i), the distance between the best model and other models (Δ_i), and evidence ratios (w_i/w_j) (Burnham and Anderson, 2002; Roberts and Luther, 2023). A $\Delta_i$between zero to two indicates substantial support for the model, four to seven substantially less support, and models > 10 have essentially no support (Burnham and Anderson, 2002). Therefore, only models with Δ_i between zero and two were considered for parameter estimation. Lastly, models with an evidence ratio of < 0.1 were not considered for further analysis (Burnham and Anderson, 2002).

3 Results

The 120 case reports in this study were from all continents (except Antarctica), and included all terrestrial vertebrate taxonomic groups. Mammals represented over half the cases in the study, followed by birds at almost one fifth of cases, while reptiles and amphibians represented a much smaller portion of the rewilding cases (Figure 1A). The majority of cases were from the global north with fewer cases from regions in the southern hemisphere (Figure 1B).

Mammals had the highest number of projects determined as highly successful projects while birds had the only project that was

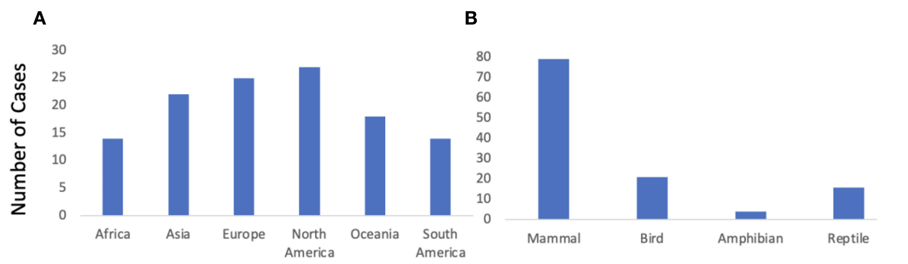

FIGURE 1
The number of case reports included in the study. **(A)** divides the number of cases by global region. **(B)** has the number of case reports by taxonomic group.

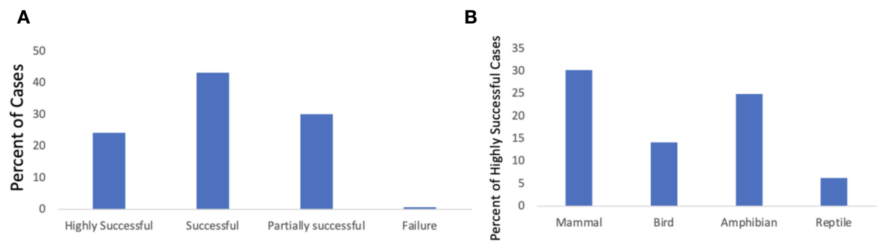

FIGURE 2
(A) The percent of case reports based on the determined success rate of the cases. **(B)** the percent of highly successful case reports for each taxonomic class in the study.

determined to be a failure. Mammals and Amphibians had the highest percentage of projects that were determined to be highly successful (Figure 2A). The greatest proportion of projects were determined to be successful, followed by partially successful, highly successful, and failures (Figure 2B, also see Supplemental Online Material (SOM) Table 2 for list of all case studies, species, threats, and success rates).

3.1 Common sociopolitical factors and threats affecting level of success

The factors that predicted success in most cases were showcasing intermediary results, meaning that a project gives reports of throughout the project, rather than just at the end (by year), pilot studies demonstrating rewilding potential (by year and class) and strong stakeholder collaboration (by year and class) (Table 3; Figure 3), all of which are part of the proof of concept success factor as defined by Segar et al. (2022). Only success factors showed $\Delta_i < 2$, and therefore were the models that predict success in most cases. The parameter estimates for these top models shows high standard error across models (Table 4), meaning that there may not have been a large enough sample size and that these success factors and guiding principles are not as related to success of a project as one might expect given the AIC values.

The top threat was land and water management activities, including hunting, over-grazing, over-fishing, intensive logging, drainage and river regulation (by class and year), but showed a Δ_i of 2.22, which is below the threshold for being one of the factors that predicted success. Based on these results, success factors, more than threats, help determine the level of success of a project.

3.2 "Guiding Principle for rewilding" affecting the level of success

Guiding Principle 9, regardless of the year of the project, class of the rewilded species, and continent on which the rewilding took place, is the Guiding Principle that best predicted rewilding success as none of the other principles were in the top models or had a AIC

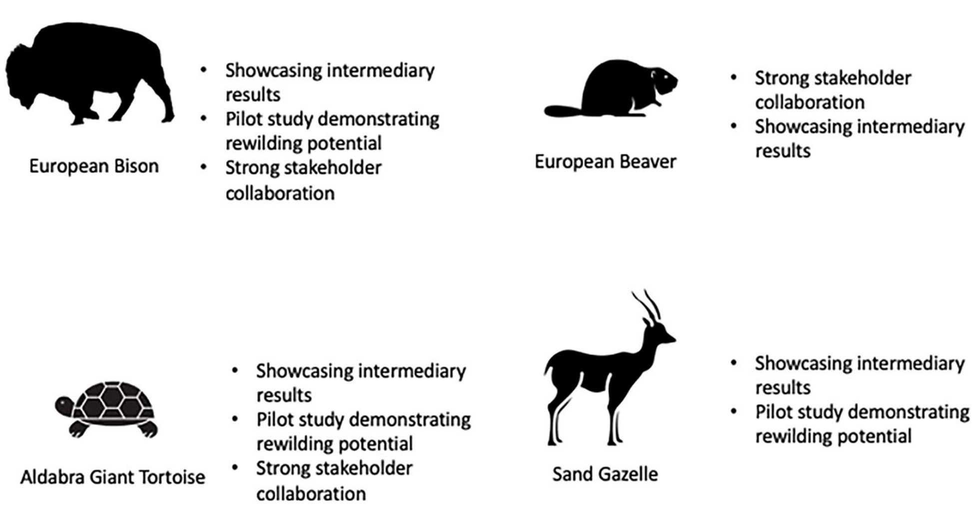

FIGURE 3
Examples of highly successful rewilding projects and their key success factors.

TABLE 3 Top models, with ΔAICc values greater than 2, of sociopolitical factors and threats, from Segar et al. (2022) that are predicted to affect the level of success of rewilding projects.

Model name	K	AICc	ΔAICc	w_i
Showcasing intermediary results (by class)	4	300.68	0.00	0.07
Pilot studies demonstrating rewilding potential (by year)	4	301.17	0.49	0.06
Pilot studies demonstrating rewilding potential (by class)	4	301.61	0.93	0.05
Strong stakeholder collaboration (by year)	4	301.96	1.28	0.04
Strong stakeholder collaboration (by class)	4	302.42	1.74	0.03

less than two. Thus, Principle 9, rewilding recognizes the intrinsic value of all species, is the top Guiding Principle for predicting rewilding success (Table 5; Supplemental Online Material (SOM) Table 2 lists all models). Guiding Principles 1, 2, 3, 5 and 10 were within the top 10 models but were separated from Principle 9 by a Null model and all of them had AIC's greater than two, thus were less likely to be associated with rewilding project success (Table 6).

4 Discussion

Our models suggest which threats to success, success factors, and guiding principles for rewilding, are likely associated with the level of success for rewilding, through species reintroduction. Specifically, the success factors of showcasing intermediary results – publicly communicating results throughout a project, not just at the end; demonstrating potential through pilot studies – conducting pilot studies utilizing the same landscape and/or species to demonstrate potential results of a larger project; strong stakeholder collaboration – working with people involved in the project and living alongside it from the beginning; and guiding principle 9 – "rewilding recognizes the intrinsic value of all species", were most strongly associated with a higher level of success of a rewilding project. All three success factors are subcategories of illustrating a proof of concept of rewilding success, which indicates this could be an important aspect of successful rewilding projects and should be considered when planning rewilding programs to help improve the odds of successful rewilding efforts. Our results of the social and political threats, success factors, and guiding principles associated with successful rewilding projects have the potential to help increase the successful outcomes of future rewilding projects.

This project assesses information from rewilding projects around the globe but we acknowledge that it can often be difficult for global analyses to be relevant to specific local projects. Thus, while our study looks at global trends as to which factors are seemingly most important for the success or failure of rewilding projects each local project has unique attributes and situations that might not be relevant under a global lens. Therefore while our findings that: publicly communicating results throughout a project, conducting pilot studies utilizing the same landscape and/or species to demonstrate potential results of a larger project, and working with people involved in the project and living alongside it from the beginning, all should have universal appeal and aid the success of future rewilding projects, they might not be right for all local situations and at the end of the day local knowledge of the ecological, sociological, and political landscape should determine the best course of action for any new rewilding project.

The determination of success in rewilding projects has historically meant biological success of the species being introduced, which usually translates to either survival or breeding success of the rewilded population over a certain period of time, such as 1 year or 5 years. The case studies used for the current study used this same definition of success. However, success of a project can mean many different things to different stakeholders, and having a definition of success that incorporates multiple perspectives at the onset of a project, if agreed upon early in the process, could help ensure that all parties are satisfied with the goals and potential eventual outcome of a project. In the present study, case study authors did not account for success in the eyes of local stakeholders, or anything beyond the original context of the biology of the study organism or ecological impacts from the introduction of that organism. Thus while the case study authors may have deemed their own project a success in biological terms, a local landowner might deem the project unsuccessful because it failed to protect their property or crops or some other resource that was important to them, which needs to be taken into consideration and addressed in future rewilding efforts if we are to garner local landowner participation and buyin to the rewilding process.

4.1 Common sociopolitical factors and threats that determine the level of success of a project

We predicted that the main sociopolitical factors that affected the level of success of a rewilding project revolved around human-

TABLE 4 Parameter estimates for best-supported models that assess success factors and threats.

Model	Estimate	SE
Showcasing Intermediary Results (by class)	0.21	0.27
Pilot Studies Demonstrating Rewilding Potential (by year)	0.18	0.27
Pilot studies demonstrating rewilding potential (by class)	0.31	0.15
Strong Stakeholder Collaboration (by year)	0.37	0.18
Showcasing Intermediary Results (by year)	0.28	0.27

TABLE 5 Top model selection of "Guiding principles for rewilding" that affect the level of rewilding success.

Model name	K	AICc	ΔAICc	w_i
Guiding Principle 9 – intrinsic value (by class)	4	301.23	0.00	0.16
Guiding Principle 9 -intrinsic value (by year)	4	301.80	0.56	0.12
Guiding Principle 9 -intrinsic value (by continent)	4	303.00	1.76	0.07
Null model Guiding Principle 9 (by year)	3	303.04	1.81	0.07

wildlife conflict and mitigation. However, we found instead that while this success factor and threat to success may be included in activities that fall under one of the named factors, human-wildlife conflict and mitigation were not explicitly the most related to the success or failure of a project. Furthermore, we found that the success factors of showcasing intermediary results, pilot studies demonstrating rewilding potential, and strong stakeholder collaboration were statistically significant to the level of success of a rewilding project. Threats were not included as important factors to consider as they did not have a ΔAICc of less than two, making them less likely to influence success than the key success factors and guiding principles.

These factors can be seen in multiple case studies from the "Global Perspectives" across the years 2008-2021, in particular cases about the sand gazelle (Soorae, 2008), Eurasian beaver (Soorae, 2011), Aldabra giant tortoise (Soorae, 2018), and European bison (Soorae, 2021) that were all reported as "highly successful" rewilding projects. The sand gazelle case used post-release monitoring after successive years of reintroduction, and modified each release method based on the results of the previous year of monitoring, each of which had a successful number of living and breeding individuals during the monitoring (Soorae, 2008) – the ability to demonstrate intermediary results and pilot studies demonstrating rewilding potential. The Eurasian beaver example also included post-release monitoring over decades to provide examples of success and evaluate what they might do better in future releases, but also worked with local hunters before the project started to make sure they would follow hunting regulations (Soorae, 2011) – indicating strong stakeholder collaboration and showcasing intermediary results.

The Aldabra giant tortoise example, one of the few reptile examples included in the "Global Perspectives", was also "highly successful" and included all three success factors. The species itself was chosen as an ecological replacement because they could be easily removed if they were shown to have deleterious impacts, scientists employed continuous research and monitoring since release, and they collaborated between the private sector, universities, and the Mauritian Wildlife Foundation (Soorae, 2018). Finally, the European bison also exhibited all three success factors, making it a "highly successful" project. This project conducted post-release monitoring, engaged in educational and public awareness activities, established mechanisms to provide benefits to the local economy, provided evidence of high post-release survival and birth numbers across multiple releases with no cases of poaching, and this project was replicated in other sites in Romania as a result (Soorae, 2021). All of these examples show that "highly successful" rewilding projects employ intermediate results based on post release monitoring as an important factor of successful rewilding.

Human-wildlife conflict and mitigation can fall under the categories of strong stakeholder collaboration (mitigation) and land and water management (Segar et al., 2022), as conflict requires stakeholders to work together to solve problems and conflict can also arise due to different land and water management practices that can affect where a species goes versus does not. Human-wildlife conflict has been shown to be present in many rewilding projects that involve reintroductions (Ramos et al., 2018; Jordan et al., 2020; Thulin and Röcklinsberg, 2020; Banasiak et al., 2021). These results do not necessarily mean that human-wildlife conflict and mitigation are not related to the level of success of a project, but rather that they are a subset of an entire suite of success factors and threats that determine the level of success of a project. Segar et al. (2022) found that the highest number of rewiding sites employed "rewilding concept appeal", "local engagement and pride", "showcasing intermediary results", and "keystone species reintroduction" as the main key success factors within the projects studied. This is slightly different than the best models we found, which included "showcasing intermediary results", "pilot studies demonstrating rewilding potential", and "strong stakeholder collaboration". Differences in results could be due to the fact that the case reports that we examined had a global lens, rather than strictly European. There may be differences in the success of rewilding projects in different parts of the world that would lead to different success factors being more or less important to the success of the project. Additionally we included a broader taxonomic group of species which might have affected the different results between Segar et al. (2022) and this study.

TABLE 6 Parameter estimates for best-supported models that assess the "Guiding principles for rewilding" that affect the level of rewilding success.

Model	Estimate	SE
Guiding Principle 9 – intrinsic value (by class)	-0.38	0.18
Guiding Principle 9 – Intrinsic value (by year)	-0.37	0.19
Guiding Principle 9 – intrinsic value (by continent)	-0.43	0.18
Null model Guiding Principle 9 (by year)	2.89	0.12

4.2 Guiding principles for rewilding that affect the level of success of a project

Only one of the guiding principles guiding principle 9, "Rewilding recognizes the intrinsic value of all species" correlated with level of success. We expected that other guiding principles would potentially be significant as they often appear in the literature and case studies (Bavin et al., 2020; Coz and Young, 2020; Drouilly and O'Riain, 2021; Thomas, 2022). While principle 9 is difficult to measure quantitatively it was not difficult to pull text about this principle out of the case reports to be included in our analyses.

Rewilding aims to restore ecosystems by allowing natural processes and wildlife to reclaim areas no longer under human management, or under minimal management, and therefore ethical considerations must be taken into account when taking on a rewilding project. Guiding Principle 9 demonstrates the importance of providing nature with its own intrinsic value, meaning humanity has the ethical responsibility to protect and respect it (Carver et al., 2021). Rewilding also poses other ethical considerations related to intrinsive value, including the welfare of animals set to be reintroduced or translocated, and as ethical values clash that can happen when moving a potentially problematic animal from one place to another (Thulin and Röcklinsberg, 2020). Finally, Guiding Principle 9 emphasizes the values of compassion and coexistence within rewilding projects, something that marks rewilding as different than a pure reintroduction or translocation (Carver et al., 2021). The focus is ecocentric, rather than anthropocentric. However, while intrinsic value is shown to be important in the success of rewilding projects, as well as a value that underpins norms in the field of conservation biology, it is not uniformly accepted in broader society. This is why it is critical to look at how principle 9 is practiced in the field and whether its existence can be assessed through stakeholder engagement.

When looking at measuring principle 9 in practice, rewilding practitioners should be focusing on the affected stakeholders' perceptions of the project itself, as well as any wildlife involved. Measuring intrinsic value here means that stakeholders see value in the wildlife outside of just the economic benefits, and goods and services, that they may provide to people (Vucetich et al., 2015; Carver et al., 2021). This could take the form of workshops, learning whether stakeholders believe that nature and any specific species involved have intrinsic value, or questionnaires to assess the values that are held by stakeholders regarding nature in general and the project specifically. Understanding the underlying values and attitudes that stakeholders have towards a project and nature, demonstrated through evaluating the existence of principle 9, are critical to knowing whether success is possible given current perceptions (Teel and Manfredo, 2010; Bennett et al., 2017; Manfredo et al., 2021). When examining the rewilding of small-bodied species like river otters and birds, it is necessary that the public recognize the intrinsic value of the species and the desire to coexist with them (Sakurai et al., 2022). Once agencies and practitioners understand whether an affected group of stakeholders believes in the intrinsic value of nature, they can work on trying to change perceptions if necessary. Thus, recognizing the intrinsic value of all species is key to rewilding success, and should be considered in future rewilding projects as a main piece to establish before a project begins. Our results show that when this principle is considered in a project, the likelihood of success increases, demonstrating the importance of incorporating social science into rewilding practice.

The ten "Guiding Principles for Rewilding" (Carver et al., 2021) were created to clarify the concept of rewilding, which can be at times be vague and all-encompassing. In comparison to the Society for Ecological Restoration principles for restoration and the European Rewilding Networks' "Global Charter for Rewilding Principles", the "Guiding Principles for Rewilding" include more social and political factors (Jepson, 2022). Narrowing down the concept to ten well-defined principles is aimed to help practitioners looking to begin rewilding projects and who are struggling with where to begin and what to include in their preliminary assessments.

While the results of our study should make an important contribution to future rewilding efforts it is important to note that the "Global Perspectives" case reports had a very low reported number of cases as "failure" – only one across 120 case studies – showing that the subjectivity of the authors' self-reports may have affected what contributes to "success" in a project. In fact, many reintroduction and translocation projects fail as translocated populations often do not survive past the first year due to inadequate space, conflict, small sample size, and acclimation to captivity, among other reasons (Bennett et al., 2012; Germano et al., 2015; Ovenden et al., 2019). In the future this propensity for failure among rewilding projects, through species reintroduction, should be taken into account when looking at self-reported successes.

4.3 Further study

The results highlight the importance of a proof of concept and local awareness of rewilding prior to implementation as critically important factors that aid in the success of rewilding projects. In addition, the activities laid out in the success factors are clear: demonstrate that a pilot study has rewilding potential, showcase that a project is having positive intermediary results, and involve stakeholders in collaborative ways throughout a project – all of these factors are sociopolitical in nature. If going into a project with these activities in place, and thinking about rewilding itself as an activity that affords wildlife and nature intrinsic value, a project is more likely succeed. Therefore, in order to improve upon the success of rewilding projects, these sociopolitical factors should be taken into account by practitioners, at least where rewilding through reintroduction is the method of choice. However, there are potential limitations to using this case report data in evaluating success factors, threats and the guiding principles due to the authors' self-assessment of success within each report. There were no specific criteria that each author had to vet their project against when determining success, and therefore each author selected the level of success subjectively. In order to make this a more quantitatively robust study, it would be of value to have case studies of rewilding that each evaluate success based on a set of pre-defined criteria, and to look at success factors, threats, and guiding principles involved in those case studies.

While IUCN's "Guiding principles for rewilding" (Carver et al., 2021) are helpful in determining what underlying principles a rewilding project should embody, there is clear need for more practical guidance in how to properly conduct a rewilding project from both the ecological and social perspectives. Following IUCN's "Guidelines for reintroductions and other translocations" (IUCN SSC, 2013), as well as "Guidelines to facilitate human-wildlife interactions in conservation translocations" (Consorte-McCrea et al., 2022) are important to set the stage for conservation translocations and reintroductions on the whole, there is a need for practical guidance on conducting rewilding projects that does not currently exist. We suggest the creation of a set of practical guidance on rewilding that takes into account both ecological and sociopolitical factors for success, and ensures that the guiding principles for rewilding are embodied in a project from the outset. This type of guidance would set rewilding projects up for success.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

SW: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration. DL: Methodology, Resources, Writing – original draft, Writing review & editing, Visualization. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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The Cornwall Beaver Project: navigating the social-ecological complexity of rewilding as a nature-based solution

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The story of the Cornwall Beaver Project is presented as the foundation of a review of the literature to consider the effects of beavers on geomorphological and hydrological processes, habitats, biodiversity, and people in agricultural landscapes in the UK. The review includes a comparison of the principles for rewilding as an approach to ecological restoration with IUCNs principles for Nature-based Solutions together with a summary of beaver reintroduction in Europe, and the impacts of beavers on hydrological and geomorphological processes, biodiversity and the human-wildlife conflict that arises from reintroduction. We note that rewilding principles require a paradigm shift in the relationship between humans and the rest of nature and a corresponding application of systems thinking to research, practice and policy. The combination of experiential and formal knowledge is assessed using a social-ecological systems framework to consider the potential of beavers to mitigate climate change impacts on agricultural landscapes in the UK and how rewilders might navigate the social complexity of beaver reintroduction to achieve large scale system transformation. We discuss the different lines of evidence about the impacts of beavers on landscapes as viewed through a system lens and conclude that: (1) beaver dams have considerable potential to store water but their ability to reduce flood risk is difficult to assess because of the complex interactions between the material available for dam construction, geomorphology, and the duration, extent and intensity of rainfall events; (2) beaver dams, especially when combined with buffer zones along water courses have considerable potential to enhance the resilience of agricultural landscapes and support a shift from intensive to agroecological farming; (3) scaling beaver reintroduction will evolve with the application of policies and practices that enhance the ability of land users to adapt and learn how to coexist with beavers. Our review proposes a low conflict strategy for rewilding with beavers that includes changes from a policy of conflict avoidance to a proactive policy to support practices that apply the tools of social-ecological systems science to the body of knowledge about the interactions between beavers and their environment.

KEYWORDS

beaver, rewilding, ecological restoration, nature-based solutions, resilience, social-ecological systems

Introduction

The Eurasian Beaver (*Castor fiber*) and its North American relative (*Castor canadensis*) are well known as keystone herbivores (Rosell et al., 2005; Janiszewski et al., 2014) whose dam building behavior creates wetlands that reduce the effects of extreme floods and droughts, capture sediment, improve water quality and enhances biological diversity (Law et al., 2016; Law et al., 2017; Puttock et al., 2017 Willby et al., 2018; Brazier et al., 2021; Larsen et al., 2021; Wohl, 2021; Orazi et al., 2022).

Rewilding (Jepson et al., 2018; Carver et al., 2021) is a specific approach to ecosystem restoration (Nelson, 2023) that emphasizes the restoration of ecosystem function through the reintroduction of apex predators such as wolves and keystone herbivores such as bison and ecosystem engineers such as beavers. Rewilding that restores the functional roles of animals in ecosystems can expand natural climate solutions (Svenning, 2020; Malhi et al., 2022; Schmitz et al., 2023). Beaver dams moderate stream flow to reduce flooding and enhance water storage (Brazier et al., 2021), they can alter wetland CO2 and CH4 flux and have the potential to increase carbon sequestration by expanding wetlands along water courses (Schmitz et al., 2023).

In addition to its potential as an approach to ecological restoration, rewilding has profound social implications. The idea of rewilding nature is extended to include the rewilding of humans to address the disconnection between humhans and nature, which is proposed as a root cause of the current global environmental crisis (Mafey and Arts, 2023). Ecosystem restoration improves human health through the provision of a wide range of ecosystem services essential for human wellbeing and simply being in nature has positive impacts on mental health (Van Volkenburg, et al., 2023). Wetlands created by beaver reintroduction may increase nature connectedness in the UK and increase the psychological wellbeing of visitors to beaver enclosures and reintroduction sites (Gandy and Watts, 2021).

Despite the social and ecological benefits of rewilding, its use as a conservation strategy in the UK faces opposition primarily from farmers concerned about loss of land and associated loss of income (Aglionby and Field, 2023). The negative impacts of beavers include flooding of crops and human settlement, and various forms of damage to trees, crops and agricultural equipment (Brazier et al., 2021). The undesirable effects of beaver reintroduction can be managed through stakeholder engagement that validates land users concerns, and designs mitigation measures together with a management support service, compensation and lethal control where necessary (Brazier et al., 2021).

The Cornwall Beaver Project (CBP) is an example of rewilding initiated by a farmer who established a beaver enclosure as the first step in a process that aimed to use beavers to reduce flooding in a downstream village and improve the conservation of biodiversity on his farm. Various forms of public engagement followed the establishment of the enclosure to address stakeholder concerns about the proposed reintroduction, create opportunities for learning about beavers and their effects on hydrology and biodiversity within the enclosure. The project proponent was also employed as the Director "Community and Land" by the Beaver Trust (beavertrust.org), a non-governmental organization created to restore beavers to their former range across Britain. The networking and knowledge sharing activities that occurred on-farm together with the broader network developed through the Beaver Trust led to the consideration of strategies for policy development to support widespread reintroduction of beavers in the UK as a measure that enhances the resilience of agricultural landscapes to climate change.

Among the rewilding literature reviewed for this case study there are only two items that referred to social-ecological systems (SES) suggesting that a deeper exploration of the concepts and applications of systems thinking might provide further insights of value to practitioners and policy makers concerned with beaver reintroduction and rewilding in general. Based on a survey of "rewilding pioneers" Hawkins (2023) proposed a SES framework for categorizing qualitative change in landscapes that contribute to the ecological and socio-cultural goals of rewilding. Collectively, these contribute to the system goal of creating "*Landscapes or social-ecological systems that are sustainable, resilient, 'wild'*" (Hawkins, 2023) that encompasses the dynamic relationship between people and nature (Berkes, 2017).

The purpose of this review is to present the experiences of the CBP as a site for learning about the effects of beavers on geomorphological and hydrological processes, habitats, biodiversity, and people in an agricultural landscape. The central issue we address is: can beavers make a significant contribution to the restoration of ecological processes in agricultural landscapes and enhance the resilience of those landscapes to climate change?

After presenting the experiences of the CBP and associated work with the Beaver Trust we compare the principles for rewilding (Carver et al., 2021) as an approach to ecological restoration with IUCNs principles for Nature-based Solutions (Cohen-Shacham et al., 2016). We then present a review of some the literature on beaver reintroduction in Europe and the impacts of beavers on hydrological and geomorphological processes, biodiversity and the human-wildlife conflict that arises from reintroduction.

The final section of the literature review presents an overview of Holling's SES framework (Holling, 2001) that was adopted as a set of principles for enhancing the resilience of ecosystem services (Biggs et al., 2012). These principles enable the integration of the scientific and practical knowledge of people involved in beaver reintroduction to consider the potential of beavers to mitigate climate change impacts on agricultural landscapes in the UK. The resilience framework also provides a way of understanding how to navigate the social complexity of beaver reintroduction and progress from local innovation to large scale system transformation (Westley et al., 2014; Moore et al., 2015). We include the application of adaptive governance concepts (Cosens and Gunderson, 2018) in our consideration of scaling as beaver range in catchments may extend across multiple jurisdictions and require the evolution of polycentric decision-making systems that match the institutional scale of catchment management with the ecological scale of beaver behavior.

The experience of the CBP and knowledge from the scientific literature are brought together in the discussion where we consider the evidence for the ability of beavers to provide an NbS for drought and flood mitigation and to enhance the resilience of agricultural landscapes. The discussion considers the matter of scaling beaver reintroduction in relation to the creation of new organizations for managing human-beaver conflict. We end the discussion with a section where we present suggestions for improving rewilding practice and policy support based on CBP experience, rewilding literature and SES concepts of adaptive governance that enable people to learn how to coexist with beavers.

The Cornwall Beaver Project

Introduction

This account of the CBP was related to Mike Jones by Chris Jones in a series of discussions in 2022 and 2023. Chris Jones is a conservation-oriented farmer who has lived and worked on Woodland Valley Farm for over 60 years and who leads the CBP with the aim of promoting the restoration of ecological functions of rivers with beavers as a strategy for reducing the impacts of farming, climate change and biodiversity loss on agricultural landscapes and riverscapes. Mike Jones used the CBP story as the foundation for this review and used the literature on beavers and social-ecological systems to consider the application of scientific knowledge to rewilding practice and policy. Mike Jones is a field ecologist who planned and implemented community-based conservation projects and is now a semi-retired educator living in Sweden. Application of social-ecological systems thinking to biodiversity conservation practice and policy was a core part of his work. The authors share a common concern for the future of agriculture under the combined effects of extreme weather and biodiversity loss on degraded agricultural landscapes and view restoration with beavers as an important step towards enhancing the resilience of agricultural landscapes.

Establishing the project

The Cornwall Beaver Project began on Woodland Valley Farm, Ladock in 2014 in collaboration with the Cornwall Wildlife Trust to consider the design and location of an enclosure for a pair of beavers with stream flow monitoring equipment, collection of baseline streamflow data for 18 months before the beavers were introduced, and the construction of an enclosure. The original idea was to determine how beavers might affect streamflow and reduce the risk of flooding in the village of Ladock located 2 km downstream. Ladock was flooded in 2012 and 2013. The frequency of flooding is expected to increase with the trend towards extreme weather as global temperatures rise. A pair of adult beavers from Derek Gow Consultancy were put into an enclosure on Nankilly stream in 2017 and began to build a dam within two days of their release. The owners of Woodland Valley see beavers as a ‘gateway’ to more extensive rewilding because of their ability to restore streams and wetlands that would attract many other species with relatively few undesirable impacts on existing land use.

In 2014, there was no way to obtain a license for the free release of beavers which was the initial aim of the project. It was obvious that we would have a very long campaign to get wild beavers back into the headwaters of the Tresillian river above Ladock and realized that getting a permit for an enclosed release was the only way to make progress towards our long-term goal of using beavers for flood reduction. Without that controlled, experimental approach, we could have wasted many years and made no progress in learning how beavers could restore ecological functions to the landscape and how that would affect farming operations. A beaver colony in an enclosure allowed research, public engagement, learning, and education to begin immediately.

Woodland Valley Farm is 170 acres (69 ha) in extent and managed as an organic grass-fed beef production system with an environmental education center for schools and universities that also serves as a conference and events center. The farm owners are founding members of the Pasture-Fed Livestock Association and regular contributors to the Oxford Real Farming conference that explores alternatives to conventional agriculture.

Nankilly stream is one of three headwater streams that combine some 200 m above Ladock to form the Tresillian river which eventually discharges into the sea via the Fal estuary some 10 miles (16 km) to the southwest. The landscape of Woodland Valley Farm and its neighbors is undulating with relatively deeply incised valleys in parts that are partially wooded. Nankilly stream and other tributaries of the Fal river have considerable potential for the free release of beavers as they provide suitable habitat in places where there is relatively little conflict with farming as most of the streams are lined with woodland.

The beaver enclosure site on Woodland Valley Farm was an 8 acre (3 ha) field called “the moor” located near the head of the Nankilly stream. The field was drained sometime during the 18th century by a large ditch on the north side that diverted most of the stream around the field. Despite the drainage, the original stream channel is still evident, and carries flowing water during high rainfall periods. The soil included a large proportion of heavy kaolinitic clay that prevented cultivation and limited use of the field to production of rough pasture. A small pond was built at the upper end of the field in 1985 to store water for livestock in the event of a repeat of the kinds of drought experienced in the 1970s. The rest of the field was planted with a mixture of birch, oak and willow trees located according to micro-site variation within the field in 1988. Once the saplings had reached a height of about 3 meters in 1994 the field was fenced and used for a small herd of free ranging pigs. The beaver enclosure occupied about 3 acres (1.5 ha) located at the upstream end of the field.

Research and monitoring

Research and monitoring are ongoing and while much of the work is unpublished it is briefly summarized by the Cornwall Wildlife Trust (2022). Published accounts of monitoring projects include a long term and ongoing hydrology monitoring project (Puttock et al., 2021) and a survey of perspectives of people in Ladock about the use of beavers for flood alleviation (Auster et al., 2022a). In addition to this published work, water quality monitoring began in 2021; an MSc thesis study on algae was undertaken; an undergraduate dissertation on silt in the beaver ponds revealed that about 270 tons of silt accumulated with 15% organic matter; and an undergraduate dissertation on the spread of standing water across the site found 2,000 cu m of accumulated water. Various surveys of biodiversity are undertaken by local naturalists including surveys of fish, tree felling by beavers, macro invertebrates, and bats.

Sharing knowledge about beavers

CBP was established with the express intent of promoting beavers and contributing to the adoption of beavers as a part of the Cornish landscape. Social media were used from the outset to support a crowd funding campaign to pay for the establishment of fencing, the animals themselves, camera traps, Bavarian beaver traps and training for project staff. Social media also played an important role in public acceptance of the idea of a beaver project in their community.

The CPB hosted innumerable visits by the public, schools, colleges and stakeholder groups, including farmers, who amongst all others were the most likely to oppose beaver reintroduction. Press releases at critical points of project development brought interest from TV, radio and newspapers. Over time, a variety of nature programs such as Springwatch, Countryfile and the documentary film maker Simon Reeves came to film the beavers.

The community outreach work of the CBP is important because any subsequent unfenced release into the Fal or other catchments will require evidence of public and landowner tolerance if not wholehearted support. In general, some people are concerned about the impacts of beaver on trees, loss of farmland to flooding, crop damage and impacts on fish. Beaver supporters generally view them as good for flood control, don't mind some trees being lost and view beaver ponds as additional habitat for fish. CBP outreach also hosted people starting their own beaver project who came to learn from CBP experience. This contributed to the establishments of other enclosed beaver projects: five in Cornwall (with two others planned) one in Devon and one in London.

Learning from beaver reintroduction sites

Going further afield the proponent of the CBP played a leading role in the development of the Beaver Trust that led to visits to beaver reintroduction sites in Bavaria, Devon and Scotland to learn more about the conflicts that can occur between free released beavers and land users.

Tay Valley, Scotland: The wild beaver population of the Tay Valley was established by escapees or deliberate release from enclosures in 2001 in a landscape of high agricultural value (Coz and Young, 2020) leading to conflict that is now being addressed by a scheme to mitigate beaver damage (NatureScot, 2021). Mitigation measures include live capture of beavers for translocation and culling. In 2022 63 beavers were destroyed under license on the Tay and another 45 were trapped for translocation (NatureScot, 2022). The latest survey from Tayside suggests that the population now comprises about 250 territories (roughly 1000 beavers) and has extended its range to the Forth valley (Campbell-Palmer et al., 2018). The Tayside experience tells us that releasing beavers into high value agricultural land without extensive prior consultation and a sound management plan is going to be highly problematic.

Danube River, Bavaria: An engineering project at a cost of one million Euro was planned to address flooding experienced by the town of Winzer in Bavaria and then extensively modified after a family of beavers established a territory upstream of the town. Hydrological studies indicated that the beavers had reduced flood peaks to the extent that a reduced engineering defense scheme was sufficient at one third of the cost of the original project (Schwab and Schmidbauer, 2003). Conflict between beavers and farmers is mitigated by a statutory 6m wide river buffer that may not be cultivated and the employment of two professional beaver control officers. Additional support is provided by an extensive network of volunteers trained in all aspects of human beaver conflict who help landowners find solutions to problems created by beavers (Schwab and Schmidbauer, 2003).

Otter River, Devonshire: In contrast to the Tayside and Bavaria cases, the beaver reintroduction on the Otter River was adopted as a formal management trial at an early stage with a license from DEFRA and the support of a major landowner in the catchment (Howe and Crutchley, 2020). A part of this trial was the implementation of a Beaver Management Group (BMG) which has representatives of government agencies, NGO's, water companies and local stakeholders (Auster et al., 2022b). The creation of a BMG is proposed as a measure for management of existing unauthorized beaver populations (Pouget and Gill, 2021) may be adopted as part of the licensing process for unfenced releases.

There were conflicts between beavers and existing land users at all three reintroduction sites and all three have evolved management systems to address the conflict, each of which is different from the other. Tayside might be regarded as the most problematic because the beavers were escapees that settled on the Tay floodplain with considerable impact on high value farming. The conflict eventually abated, and culling and translocation licenses are now available for farmers suffering significant damage. In the case of Bavaria, the initial reintroduction was regarded as beneficial as a flood mitigation tactic and conflicts with farmers and other land users was mitigated by the evolution of an effective beaver management system. Aspects of the Bavarian experience we adopted for managing human-beaver conflict in the Tay valley (NatureScot, 2021).

Some relevant literature

Here we present some of the scientific and UK policy literature that is relevant to the long term aims of the CBP and that adds to the knowledge obtained during the life of CBP and associated networking. This includes rewilding with beavers as an NbS, a short account of the history of beaver reintroduction, a summary of beaver effects on ecosystem process and biodiversity, and ways of managing conflicts between beavers and other land users. We then present an SES framework, its use as an approach to enhancing the resilience of ecosystem services and its use for scaling local innovation.

Beavers as a nature-based solution

The ecosystem services of streamflow regulation, water quality improvement and biodiversity conservation provided by beavers make them a useful alternative to mechanical methods of restoration (Palmer et al., 2014; Brazier et al., 2021) and thus an NbS (Cohen-Shacham et al., 2016) to the societal challenges associated with global environmental change (Steffen et al., 2015). Freshwater and riparian environments are widely threatened (Reid et al., 2019) and the global abundance of freshwater species have declined by 84% since 1970 (WWF, 2020). Wetlands created by beavers in agricultural landscapes mitigate the adverse socio-economic impacts on five of the nine planetary boundaries that define a safe operating space for human society (Richardson et al., 2023). The five transgressed boundaries (climate change, biosphere integrity, land system change, freshwater system change and biogeochemical flows) will be directly and positively affected by beaver dams. The keystone role of beavers as ecosystem engineers suggests that as an NbS they can make a substantial contribution to the restoration of ecosystem health needed to keep global warming below 1.5°C and secure a livable future for humanity (Pörtner et al., 2023).

Nature-based solutions (NbS) as defined by IUCN (Cohen-Shacham et al., 2016) is a catch-all concept that covers various forms of ecosystem management, ecosystem restoration, ecosystem-based responses to climate change and disaster, green infrastructure, and area-based conservation. The intention is that NbS address societal challenges such as food and water security, health, and climate related risks. Although rewilding is a form of ecological restoration and therefor fits within the NbS framework, rewilding is different from NbS in some fundamentally important respects. Principles common to NbS (Cohen-Shacham et al., 2019) and rewilding (Carver et al., 2021) include landscape scale ambition, the need for adaptive approaches for the management of dynamic systems, and the integration of multiple forms of knowledge in the design of interventions. While NbS are strongly focused on ecosystem services and addressing societal challenges, rewilding emphasizes enhancement of ecosystem resilience, the intrinsic values of nature and a paradigm shift in the coexistence of humans and nature. Rewilding does not address societal challenges except for principle five (Carver et al., 2021) which says that rewilding can act as a tool to mitigate climate impacts.

The differences between NbS and Rewilding are significant in that it represents a shift from the "Nature for people" to the "People and nature" conservation paradigm (Mace, 2014). This shift from an anthropocentric to an ecocentric relationship between humans and nature requires an understanding of SES and related concepts such as resilience, adaptation, and transformation (Folke et al., 2010) and frameworks for their application to policy and practice.

Beaver reintroduction

Beavers were probably hunted to extinction in Britain by the 12th Century and in Scotland by the 16th Century (Lee, 2015). Beavers were mainly hunted for fur, castoreum (an oily secretion from the anal gland that is used in food and medicine) meat and the tail that was prepared and eaten like a fish on Friday's (Nolet and Rossell, 1998). Beavers were returned to the wild in Argyll, Scotland in 2009 (Coz and Young, 2020) and discovered in the wild on the River Otter, Devonshire in 2014 (Brazier et al., 2020). Subsequently reintroductions under controlled conditions have occurred at eleven sites within the UK (The Wildlife Trusts). Similar patterns of hunting to extinction followed by reintroduction, initially for hunting, and increasingly for ecological reasons since the 1970s, occurred throughout western Europe (Nolet and Rosell, 1998). Reintroduction in Europe has returned beavers to much of their original range and the population of *C. fiber* numbered about 1.5 million individuals by the early 21st Century (Halley et al., 2012).

Effects of beavers on ecosystem process

Beaver dams create wetlands that reduce the effects of extreme floods and droughts (Larsen et al., 2021; Ronnquist and Westbrook, 2021), and have the potential to restore UK wetlands, most of which have been drained or reduced to a polluted state and are dependent on artificial management (Howe, 2020). Beaver dams collect sediment that rebuilds channelized rivers and restores their hydrological functions (Brown et al., 2018; Brazier et al., 2021; Wohl, 2021) to the pre-anthropocentric conditions that were once common in Europe and degraded since the mid Holocene by agriculture and industrialization (Brown et al., 2018). Sediments in beaver dams act as sinks that affect different aspects of various biogeochemical cycles including nitrogen, phosphorous and organic carbon (Puttock et al., 2018; Brazier et al., 2021). Nutrients retained in pond sediments are taken up by plants in and around the pond, establishing local nutrient cycles and further slowing the movement of nutrients through the landscape (Rosell et al., 2005) reducing the risk of eutrophication of rivers and lakes and associated loss of biodiversity and water quality (Carpenter et al., 1998). The effects of beaver ponds on nutrient cycles are complex and dynamic, varying with dam wall porosity and pond age (Puttock et al., 2018; Brazier et al., 2021). In the western US, wetland restoration using beavers and beaver-like dams has grown rapidly since 2006 in response to concern about undesirable climate change effects to the hydrology of streams and rivers (Pilliod et al., 2018; Dittbrenner et al., 2022), prompting the US Fish and Wildlife Service to publish a comprehensive guideline for the use of beavers in restoration projects (Pollock et al., 2023).

Effects of beavers on biodiversity

Tree felling and dam building activity by beavers opens woodland canopy, creates wetlands, and changes stream bed morphology providing new habitats and increasing biological diversity (Law et al., 2016; Law et al., 2017; Willby et al., 2018; Howe, 2020; Brazier et al., 2021; Larsen et al., 2021; Wohl, 2021; Orazi, et al., 2022). Law et al. (2016) found that beaver ponds increased species richness at the landscape scale in Scotland. A twelve-year study of changes to an agricultural landscape in Scotland following the introduction of beavers showed an increase in plant species diversity and spatial heterogeneity (Law et al., 2017). A comparison between beaver ponds with adjacent wetlands in Sweden found significantly greater heterogeneity of habitats and greater species divers (Willby et al., 2018). Woody debris increases the complexity of streambed morphology creating habitat for invertebrates and amphibians with additional benefits for fish populations (Brazier et al., 2021). In Germany a comparison of beaver ponds with rivers and adjacent woodlands in a protected area found significantly more species in beaver pond habitats. Eight of the species found in this study were only found in beaver ponds (Orazi et al., 2022). In addition to these site-specific cases from the UK and Europe, Brazier et al. (2021) provide an extensive review of the changes to habitats and biodiversity that result from beaver activity.

Managing beaver-human conflict

Reintroduction of a long absent species to a landscape inevitably creates conflict with human land users and requires a period of social learning and adaptation (Cundill et al., 2011) to achieve a state of "Renewed Coexistence" (Auster et al., 2023). Conflicts and remedies for damage including dam removal, flow device measures to lower water levels, tree protection, and compensation for loss of land and crops are summarized by Brazier et al. (2021) from several sources. Gandy and Watts (2021) emphasize the psychological effects of anxiety and stress on landholders who suffer loss and the need for this to be understood, validated, compensated, and mitigated to reduce conflict. Conflicts between beavers and other land users at beaver reintroduction sites in England and Scotland extend to disagreement, mistrust, and polarization of views among landholders and beaver advocates (Inman, 2021).

Based on their study of beaver-human conflicts in Scotland Coz and Young (2020) argue that conflicts over reintroduction can be reduced by discussions among actual and potential stakeholders to agree a long-term landscape scale plan. Studies of the experience of interactions among stakeholders of the River Otter Beaver Trial and the Tamar Beaver Management Group led Auster, Barr and Brazier (2022) to conclude that collaborative groups for managing the coexistence between humans and beavers are emerging. Auster et al. (2023) emphasize the dynamic adaptive nature of beaver management groups and the need for flexible policy to support the process of humans learning how to coexist with beavers.

Accounts of the 30-year history of beaver reintroduction in Bavaria provide an example of how conflict management leads to the evolution of a system that enables coexistence between beavers and other land users (Schwab and Schmidbauer, 2003). Beaver management practices in Bavaria (Schwab and Schmidbauer, 2003; Nairne, 2019) include a statutory no cultivation zone, devolved governance systems that enables local decision making; a loss compensation scheme, a large network of "beaver consultants" to assist land users experiencing problems with beavers and culling. Some of these practices were incorporated into Scotland's Beaver Mitigation Scheme which provides government grants to mitigate undesirable dam building effects and to create various kinds of stream margin to promote coexistence between beavers and humans (NatureScot, 2021).

Social-ecological systems

The social-ecological systems (SES) framework or panarchy (Holling, 2001; Gunderson and Holling, 2002) provides a set of simple heuristics for developing mental models of evolutionary processes in human-nature systems that can be applied to individual farms, ecosystems, and landscapes. The panarchy is the foundation of ecosystem stewardship (Chapin, 2010) which emphasizes, restoration, and transformation as responses to the accelerating degradation that has arisen as the unintended consequences of modern management practices. Given the complexity of rewilding and nature-based solutions of which rewilding is a subset, the applications of "resilience thinking" (Folke et al., 2010; Curtin and Parker, 2014; Folke, 2016) seems to offer a useful approach to navigating the changes that rewilding will bring to landscapes that are highly modified to enhance the production of goods for human consumption. Virapongse et al. (2016) provide additional information about the SES framework and its ability to support transdisciplinary approaches that develop novel solutions to environmental management challenges by enhancing resilience.

Holling's panarchy comprises the adaptive cycle at three levels of scale to represent a hierarchical arrangement of systems nested within systems and the interactions between them. Small scale systems tend to change rapidly and may lead to change at higher levels of scale, large scale systems tend to resist change and provide stability over longer time frames. Key features of the continually changing adaptive cycle are the social and ecological potential for the system to change i.e., the quantities and qualities of all the social and ecological parts of the system; the dynamic connections between those parts i.e., the feedback interactions among them; and resilience which is a property that emerges from the interactions between the system's parts. The dynamic nature of systems and their different potentials for change determine what will or will not work in any given place and requires site specific planning using tools such as Wayfinder (Enfors-Kautsky et al., 2021) that are derived from the panarchy framework. Interactions between adaptive cycles at different levels of scale can lead to different outcomes. Change in small systems such as a genetic change, social or technological innovation can cascade upward ultimately leading to large scale change. In addition to resisting change large scale systems are a source of the social and ecological components necessary for restoring degraded systems. In the context of production landscapes, the ability of large-scale systems to provide stability and components for the restoration of degraded landscapes is undermined by land use practices that simplify systems to enhance their production capacity at the expense of their capacity for self-maintenance and renewal

(IPBES, 2019). The outcome of cross-scale interactions will be affected by external events such as climate change, energy decline (Hagens, 2020) and markets for ecosystem products among others. Collectively, these external events will affect land use, food and water security where the effects will vary according to the social and ecological context of a specific place.

SES and ecosystem services

Biggs et al. (2012) propose seven principles for enhancing the resilience of ecosystem services (Table 1) based on Holling's adaptive cycle and panarchy (Holling, 2001; Gunderson and Holling, 2002). These principles provide a useful way to consider beaver reintroductions within both "Nature for people" and "People and nature" conservation paradigms (Mace, 2014), and think about beaver reintroduction as a paradigm shifting process. Viewed from the "Nature for people" perspective, beavers produce multiple ecosystem services with values of individual services estimated at millions to hundreds of millions of US dollars (Thompson et al., 2020). Viewed from the "People and nature" perspective, beaver reintroduction is a complex process that requires policies and practices to support site specific approaches that integrate land use, and land users with the ecological characteristics of a place.

TABLE 1 The seven principles for enhancing the resilience of ecosystem services based on Biggs et al. (2012).

Principle	Brief Explanation
1. Maintain redundancy and diversity	Diversity comes in many forms: genes, species, landscape patches, cultural groups, livelihood strategies and governance institutions. Diversity enhances the potential of a system to change. Redundancy reduces the risk of systemic collapse by providing options for adapting to a changing environment such as rising temperatures and weather extremes associated with global warming.
2. Manage connectivity	Connectivity refers to the manner and extent to which species or social actors can move across a landscape and affects ecosystem services by affecting the spread of disturbance and recovery after disturbance.
3. Manage slow variables and feedbacks	The slow variables of a system determine its underlying structure and provide the stability necessary for the sustainable production of ecosystem services like food, fiber, fuel, livestock feed and drinking water that are essential to human wellbeing. Feedbacks regulate the relationships between variables within a system; reinforcing feedback supports increase which is regulated by balancing feedback that slows or stops the increase
4. Foster understanding of social-ecological systems as complex adaptive systems	This principle requires an understanding of the properties of complex adaptive systems (CAS) among scientists, policy makers and managers. A key part of a CAS perspective is recognition of the evolutionary change that occurs from the interaction between the parts of a system and the environment within which it occurs.
5. Encourage learning and experimentation	Learning is both an individual and social process that is essential for adapting to the incomplete knowledge and unpredictability that are features of CAS
6. Broaden participation	Encouraging the participation of all stakeholders is a key part of social learning and adaptation as it promotes transparency and knowledge sharing leading to collaboration as opposed to conflict
7. Promote polycentric governance systems	Polycentric governance is a way of managing natural resources that occur across multiple jurisdictional boundaries so that the scale at which ecological processes operate is matched by the scale at which decisions affecting that resource are made

An SES perspective is necessary to evaluate the trade-offs between different ecosystem services that consider the need to maintain the productive capacity of land by paying attention to the "slow variables" of soil and water as well as produce the food, fiber, fuel, and feed necessary for human wellbeing. The undesirable consequences of an inability to adopt a CAS perspective and consider the implications of trade-offs is well supported by documentary evidence (Holling and Meffe, 1996).

SES and scaling beaver reintroduction

In addition to providing a framework for enhancing the resilience of ecosystem services, the panarchy (Holling, 2001; Gunderson and Holling, 2002) provides a way of understanding how innovative ideas such as use of beavers for NbS can be scaled from experimental enclosures and reintroduction sites. There are three aspects to the process of scaling. Scaling out (Westley et al., 2014) is a process whereby interested groups learn from the experiences of others and decide to duplicate experimental beaver enclosures and reintroductions. Scaling up requires changes in the laws, rules and policies (Westley et al., 2014; Moore et al., 2015). Scaling deep (Moore et al., 2015) is about changing the cultural values and beliefs that affect the relationships among stakeholders and their various land uses.

Scaling up and scaling deep recognize that social innovation is a complex, emergent, and largely unpredictable process that involves interactions across the scales of Holling´s panarchy (Westley et al., 2014). Scaling deep is the same as creating a paradigm shift while scaling up can be achieved by applying lower-level levers that change rules, laws and policies that affect things like subsidies, devolution of authority and system goals (Meadows, 2009). The three kinds of scaling processes are interrelated (Moore et al., 2015) and while scaling out provides the foundation for change, scaling up and scaling deep may need to be managed interdependently to both create and exploit opportunities for change. To scale up organizations need to learn from their experience of scaling out and scaling deep and to develop the stamina necessary for leadership to prevail (Moore et al., 2015). O'Brien and Sygna (2013) propose a three spheres model of transformation that is like the three scales of Moore et al. (2015). O'Brien and Sygna (2013) suggest that effective practical action begins at the personal level with a change in beliefs, values, worldviews and paradigms. This enables engagement at the political level to change the systems and structures necessary to support practices that respond effectively to a given problem. Amel et al. (2017) explain why humans find it difficult to change environmentally destructive behavior and propose a broadly equivalent process of influencing change that begins at the personal level. In summary, all three perspectives on change process recognize the need for change at the personal level as a requirement for success in influencing others at higher levels of a social hierarchy.

Scaling beaver reintroduction as an innovation in landscape management requires land users to learn how they can coexist with beavers (Auster et al., 2023). This learning process involves the experimentation necessary for social learning (Cundill et al., 2011) broadening participation and polycentric governance required to enhance the resilience of ecosystem services (Biggs et al., 2012), all of which are essential components of learning how to coexist so that rewilding with beavers can proceed. Scaling up from enclosures and reintroduction sites to river catchments that cross jurisdictional boundaries requires consideration of the evolution of polycentric systems of adaptive governance (Cosens and Gunderson, 2018) that match institutional scale with ecological scale to manage the uncertainty that arises from SES interactions across multiple scales of time and space.

Butler et al. (2021) proposed an adaptive governance framework for rewilding that sets out the steps that might be taken to acquire a "social license to operate" a rewilding project and then continually adapt management practices as land users learn about the changes that unfold because of the interactions between them, the introduced species, and the ecosystem. This adaptive governance approach to rewilding is an advance over the IUCN Guideline for rewilding (IUCN, 2013). The adaptive governance approach addresses concerns raised by (Jepson et al., 2018) about cultural differences among stakeholders and the need to avoid projects designs that deliver pre-determined targets. Butler et al. (2021) note that adaptive governance is an evolving concept that should not be treated as a blueprint for rewilding and that while it increases costs in the short term it avoids the costs of acute or long-term conflict with negative impacts on biodiversity and human wellbeing.

Discussion

Beavers as an NbS for drought & flood mitigation

Do beaver dams provide an effective natural solution to problems of flooding and drought in agricultural landscapes?

In common with other hydrological studies (Larsen et al., 2021; Ronnquist and Westbrook, 2021) stream flow monitoring at the CBP site showed that beaver dams can significantly reduce peak flow (Puttock et al., 2021). Using this evidence to develop an effective strategy for flood risk reduction is complex because of the interaction between beavers, the dams they build, the landscape within which they occur and rainfall. The height and porosity of a dam depends on the materials available for construction (Ronnquist and Westbrook, 2021). The shape of the valley floor determines how much water is held behind the dam wall (Larsen et al., 2021). This varies with the amount of dam wall freeboard and diversion of water across floodplains (Ronnquist and Westbrook). Narrow valleys and incised streams will not hold much water. Flood risk mitigation is further complicated by the duration, extent and intensity of rainfall in relation to the location of beaver dams as well as the antecedent catchment wetness (Breinl et al., 2021). Scaling the CBP to other streams in the Tresillian catchment above Ladock is possible and may avert a significant number of potential flood events but as with all complex systems, outcomes are uncertain because of the interactions between the components of the system: in this case weather, geomorphology, beaver behavior, and available dam construction materials. Mechanical flood prevention measures suffer the same uncertainties associated with rainfall and soil (Breinl et al., 2021) as beaver dams.

While the ability of beaver dams to prevent downstream flooding is uncertain, their ability to conserve water is considerable (Pilliod et al., 2018; Dittbrenner et al., 2022; Pollock et al., 2023). Water storage capacity in the UK has reached levels where some parts of the country may run out of water within the next 20 years (National Audit Office, 2020). Stabilization of hydrological flows will become increasingly important as floods and droughts become more frequent because of global warming (Garner et al., 2015; Environment Agency, 2022).

Beavers and the resilience of agricultural landscapes

To what extent can the activities of beavers, confined to the streams, rivers and wetlands of drainage basins enhance the resilience of agricultural landscapes? This is a key question raised by Howe (2020) in reference to point source pollution of waterways and the widespread degradation and alteration of landscapes in England.

The social-ecological framework and its application to the concept of ecosystem services (Biggs et al., 2012) provides the holistic perspective that Howe (2020) suggests is needed to fully understand the ecological and biodiversity benefits of beavers. Howe (2020) also notes that reintroduction of beavers on its own cannot reduce the intense pressure on river catchments that need to be addressed at source to restore ecosystem function to headwater catchments. Much of the holistic perspective that Howe seeks may be found by developing an understanding the importance of the relationship between "slow variables", "fast variables" and feedback that is necessary to maintain or enhance the resilience of ecosystem services (Principle 3 in Table 1).

The climate and landscape processes that form soil and river catchments together with their wetlands are entities that change over millennia, unless altered or degraded by human activity which has accelerated exponentially over the last 200 years (Rees, 2020) because of the huge amounts of surplus energy supplied by fossil fuels (Hagens, 2020). Soil loss is a universal problem caused by farming (FAO and ITPS, 2015) and has contributed to the downfall of civilizations since the invention of the plough (Montgomery, 2008). Climate change is advancing rapidly (IPCC, 2023) and at a global level, the availability of water is becoming critical (GCEW, 2023; Naddaf, 2023). In the language of the SES framework, human economic activity is a fast variable exerting reinforcing feedback that is undermining the stabilizing influence of the Holocene climate, soil formation and hydrological cycle that biodiversity and humans are dependent on. Unless society establishes balancing feedback by setting a limit on economic growth (Daley, 2015; Farley and Voinov, 2016; Rees, 2020; Herrington, 2022), nature will impose limits through the synergistic effects of polluted atmosphere and degraded hydrological systems, and a decline in the qualities and quantities of climate, soil, water and biodiversity necessary for sustainable farming.

Beavers have the potential to play a significant role in restoring some landscape function to the pre-anthropocentric conditions that were once common in Europe and degraded since the mid Holocene by agriculture and industrialization (Brown et al., 2018). Beaver dams provide crucially important balancing feedback that contributes to ecosystem stability (Larsen et al., 2021) that given time can restore floodplains degraded by deforestation and arable agriculture (Brown et al., 2018). Beaver activity restores channelized water courses with low biodiversity turning them into wetlands with increased biodiversity in a relatively short period because of the interactions between the beavers, the hydrological, geomorphological and land use features of the environment within which they are released and the response of other species to the new environment created by the beavers (Law et al., 2016; Gaywood, 2017; Willby et al., 2018; Brazier et al., 2021).

The site-level restoration achieved by beavers can, as in the case of Bavaria (Schwab and Schmidbauer, 2003) be scaled out to increase connectivity within landscapes through the creation of a riparian buffer zone that reduces conflict between beavers and farmers. The combination of beaver created wetlands and corridors would complete two of the three-stage, core-corridor-carnivore model of rewilding (Soulé and Noss, 1998; Carver et al., 2021). Observation of land use by beavers in Bavaria suggest that the 6m buffer could be increased to 20m and eliminate 95% of the conflict as beavers only rarely travel more than 20m beyond water (Interreg, 2019). Such buffers would provide the basis for extensive restoration that increases biodiversity and soil organic matter and uses the soil to improve water quality by removing fertilizer and chemicals from agricultural run-off (Puttock et al., 2017; Puttock et al., 2018). The creation of buffer zones between beavers and farmland is consistent with the DEFRA's new plan for delivering clean and plentiful water (DEFRA, 2023), although beavers are not mentioned in this "integrated" plan.

The creation of corridors along water courses represents a "land-sparing" approach to reconciling biodiversity conservation and agriculture. Collas et al. (2022) found strong evidence for a land sparing approach in England and Grass et al. (2019) argue that land-spared corridors in agricultural landscapes allows species to move, saving them from extinction in hostile areas to maintain the resilience of ecosystem services. Land-sparing agri-environment schemes in Europe were found to increase the abundance and diversity of arthropods in agricultural landscapes (Marja et al., 2022). Soil dwelling arthropods play an important role in soil nutrient cycling and maintaining soil structures that reduce loss from erosion (Culliney, 2013). Plant dwelling arthropods (insects) play a critical role as pollinators of agricultural crops (Jankielsohn, 2018). Arthropod decline is due to land conversion for agriculture and use of chemicals (Hierlmeier et al., 2022). The buffer zones along water courses can be regarded as "semi-natural land" in the three-compartment model of the land use framework recommended in the National Food Strategy (Dimbleby, 2021). The process of sustainable intensification (Pretty, 2018) that ultimately aims to restore ecological processes in agricultural landscapes can be applied to high and low yield farmland in Dimbleby (2021) classification. The biodiversity refugia created by beaver wetlands and corridors as semi-natural lands within high and low yield farmland could become a significant source of the biodiversity necessary to restore ecological processes.

An SES perspective on Howe's concern about the limited ability of beavers to restore ecological function to ecosystems in the UK, recognizes a need to shift from intensive "Green Revolution" agriculture towards agroecological methods of farming (Bezner Kerr et al., 2023) with the aim of reducing soil and water loss and greenhouse gas emissions while maintaining food security (FAO, 2018). Soil, water, and nutrient loss increase with the duration and intensity of rainfall (FAO, 2019). Greenhouse gas emissions are increasing the rate of global warming and the occurrence of extreme weather (IPCC, 2023). Food production accounts for approximately 25% of global GHG emissions of which about half comes from crop and livestock production (Ritchie, 2019). Collectively the combination of climate change, soil water and nutrient loss are reinforcing feedback driving a vicious cycle of degradation that undermines the basic requirement of a healthy soil needed to maintain civilization. The decline in arthropods that maintain soil health because of agricultural practices accelerate the degradation process. Despite being confined to wetlands and watercourses beavers have considerable ability to restore the regulating ecosystem services that are essential for sustainable agriculture and the wellbeing of society.

Scaling beaver reintroduction

Overcoming the problems of human-beaver conflict is central to the problem of scaling the reintroduction of beavers for restoration of ecological process in landscapes where humans have no experience of coexisting with beavers. In this section of the review, we reflect on the different aspects of scaling described in the SES literature and based on experience in Bavaria and Scotland, suggest that human-beaver coexistence will emerge. The process of emergence will be constrained until there is a change in the current policy mindset.

The CBP has played a leading role as a source of knowledge that enabled others to initiate similar projects in other parts of Cornwall and elsewhere in England. This is an example of "scaling out" a social innovation (Westley et al., 2014; Moore et al., 2015) where beaver enclosures are being replicated. The next step of moving from beavers in an enclosure to free-ranging beavers, is a process that will involve a combination of "scaling up" (Westley et al., 2014; Moore et al., 2015) and "scaling deep" (Moore et al., 2015).

The experiences of the Otter River reintroductions provide an example of limited scaling up where human-wildlife conflict and the research that followed an unlicensed reintroduction eventually resulted in beavers being declared a protected species by the Department for Environment Food and Rural Affairs (DEFRA, 2022a) together with the issuance of guidelines and rules for their management (DEFRA, 2022b). While this may provide some stability to the conflict between land users and beaver supporters, these laws, policies, and guidance are a long way from enabling the rewilding goals of restoring ecological function to landscapes (Carver et al., 2021) or an NbS goal of using beavers to improve the hydrological characteristics of rivers as drought and flood mitigation measures. The fact that the legalization of the Otter River was forced by public sentiment in favor of allowing the beavers to stay (Crowley et al., 2017) is an indication of how unwilling DEFRA are to support widespread beaver reintroduction.

The changes in beaver management described in Bavaria (Schwab and Schmidbauer, 2003), England (Auster et al., 2022b; Auster et al., 2023) and Scotland (NatureScot, 2021) illustrate the interdependent nature of scaling and adaptive governance and the CAS concept of emergence whereby new structures and processes emerge through the interactions between the components of a system. The reproductive capacity of beavers means that their need for habitat can grow rapidly with consequences for other parts of a river basin as in the case of Tay Valley (Campbell-Palmer et al., 2018). As beavers spread and people learn about their effects on ecology and land use economics, institutional changes will occur to govern the interactions between these components of a landscape.

Scaling out because of beaver reproduction and the activities of beaver supporters together with learning about the interactions within a landscape, will cause the emergence of new laws, policies and practices that further enable and formalize the coexistence between beavers and humans. If the range of beavers extends beyond the boundaries of a local authority, some form of polycentric governance arrangement may emerge so that different authorities can manage beavers to meet commonly agreed goals. Progress in scaling out and scaling up will be constrained until a paradigm shift in the mental models of policy and decision makers has occurred. This deep scaling (Moore et al., 2015) addresses the foundational beliefs, values and assumptions from which laws and policies emerge (Meadows, 2009) and would address things like the economic and food production goals that are driving intensive agriculture and undermining the resilience of agricultural landscapes. Once the goals of a system are changed, it will reorganize to meet the new goals (Meadows, 2009).

Improving practice and policy for beaver reintroduction

The CBP experience of beaver reintroduction, together with the available scientific evidence on the management of human beaver conflicts and our knowledge of SES concepts suggests that application of adaptive governance by policy makers and the use of SES planning tools would reduce human beaver conflict and enhance the resilience of agricultural landscapes. Effective policy support requires a mindset change that recognizes the value of bottom-up processes for resolving complex problems.

Despite the barriers to rewilding identified by Aglionby and Field (2023) the interest in beaver reintroduction as a method of restoring resilience to agricultural landscapes is growing. There were five fenced enclosures in England in 2017 and about 40 in 2022 with more planned. Beavers escape from fenced sites and the wild beaver population is growing. There are now 11 rivers (Tamar, Taw, Exe, Otter, Bristol Avon, Wye, Dyfi, Kentish Stour, Dorset Stour, Clyde and Forth) with wild beavers. Among the barriers to rewilding identified by Aglionby and Field (2023) conflict between stakeholders and a muddled policy environment stand out as two broad and interrelated categories relevant to beaver reintroduction. The policy environment is muddled by the conflicting demands of stakeholders, the need to balance biodiversity conservation with farming and the need enhance the resilience of agricultural landscapes, and farming to climate change. In terms of SES thinking a defensive policy represents a rigidity trap (Scheffer and Westley, 2007; Carpenter and Brock, 2008) where conflict among the stakeholders based on locked in thinking leads to stasis when rapidly changing environmental conditions require change.

Applied adaptive governance

As a "pioneer farmer" (Thomas, 2022) the CBP favors a low conflict approach to beaver reintroduction that avoids flat landscapes with high value farmland as a sensible way to proceed. This would underline governments commitment to the farming industry, disarming the opposition to beaver re-introduction demonstrated by the National Farmers Union (NFU, 2022) and avoid wasting conservation efforts that attempt to return beavers to high conflict catchments. A proactive low conflict policy would reduce the pressure from "guerilla rewilders" (Thomas, 2022) who might otherwise release beavers in landscape with high agricultural potential and polarize the public dialogue about rewilding.

A low conflict approach would start with the formation of local groups that represents stakeholders at potential reintroduction sites and engage them at the outset in the development of a site-specific plan. Enfors-Kautsky et al. (2021) describe a participatory process for an SES assessment that includes a scenario component to explore plausible future changes that might emerge following a reintroduction. The assessment process and scenarios would provide a basis for decision-making by stakeholders about if, when and how to proceed with a proposed beaver reintroduction. The "Wayfinder" assessment and planning method described by Enfors-Kautsky et al. (2021) concludes with a section on adaptive management that enables stakeholder to navigate the changes that emerge following a reintroduction. This bottom-up approach to planning meets Howe's (2020) requirement for site specific planning in places where land users are amenable and treats each reintroduction as an experiment from which the outcomes (short term effects) and impacts (long term effects) are learned. Learning how to think in terms of SES is a process that requires some unlearning of old habits of thought based on reductionism as well as learning about the dynamics of complex adaptive systems (Rogers et al., 2013). The use of a participatory SES assessment in planning beaver reintroduction and their contribution to landscape resilience would improve the assessment of the risks of systemic failure that arise from the accumulative impacts of humans on landscapes (Wassénius and Crona (2022).

Learning how to apply adaptive governance and manage beavers (or any other kind of reintroduction) can address the barriers to rewilding identified by Aglionby and Field (2023). This would include the provision of facilitation and advisory services to support emerging beaver management groups until they have learned the techniques for themselves. Adaptive governance concepts might also be usefully applied by "armchair rewilders" and "policy entrepreneurs" (Thomas, 2022) to develop the social, political and resource mobilization skills necessary for influencing policy Westley and Antadze (2010). Learning these skills "*could be critical in shaping the UK conservation agenda for years, or even decades, to come.*" (Thomas, 2022).

Policy support

Working together and learning new techniques necessary to establish a beaver reintroduction requires an investment of time and money by stakeholders. It is difficult to imagine collaboration happening without support from government, unless undertaken by wealthy landowners or NGO's with a strong donor base. For those who can afford them, beaver management groups might successfully implement a beaver reintroduction, but undermine social equity by excluding other groups with good potential for beaver reintroduction without the resources to form a management group. This inequity may promote conflict instead of the consilience needed for large scale beaver reintroduction.

One of the conditions necessary for adaptive governance to emerge is a supportive policy environment (Armitage et al., 2009) where the role of policy is to learn about governance of complex systems and to protect the conditions of emergence (Ruitenbeek and Cartier, 2001). A change in DEFRA policy for beaver reintroduction from passive conflict avoidance to proactive support that empowers local management groups to learn how to manage conflict is required for beaver rewilding to progress from isolated enclosures and small-scale reintroduction. Recent government publications suggest that this shift in policy from top-down to support for bottom-up planning is happening through the Environmental Land Management Scheme (ELMS) in the DEFRA's agricultural transition plan (DEFRA, 2020). The ELM scheme (DEFRA, 2020) addresses biodiversity conservation, flood mitigation and diffuse water pollution which are problems to which beavers provide an NbS. The Environment Food and Rural Affairs Committee Report (EFRAC, 2023a) summarizes many of the concerns about beaver reintroduction and measures that can be taken to address those concerns based on lessons learned in the UK and Europe. The ELM scheme proposed in the agricultural transition plan DEFRA (2020) includes changes in subsidies that could enable farmers to learn how to coexist with beavers, but full details for implementation have not been released (Aglionby and Field, 2023). Government's response to the species reintroduction committee (EFRAC 2023b) affirms government's aims for achieving biodiversity targets through habitat restoration and corridors and recommends budgetary support through ELMS.

While government support for rewilding in general may be not be forthcoming (DEFRA, 2023), there are signs of a shift in policy direction that would support the emergence of beaver management groups and enable coexistence between beavers and humans. It remains to be seen how this support will be provided and what aspects of beaver reintroduction it will support.

Conclusion

The intention of the CBP was to rewild the Tresillian river with beavers to reduce the incidence and severity of flooding in Ladock village, as an NbS to a problem that is conventionally addressed with engineering solutions such as dams and levees. The accumulations of sediments and biodiversity benefits that arose from the creation of the beaver dams in the CBP enclosure are emerging over time. The research and monitoring information being collected at the CBP enclosure are consistent with the outcome of beaver reintroduction on the river Otter (Brazier et al., 2021) and a considerable body of evidence in the scientific literature on the biological, hydrological, and geomorphological benefits of beavers.

Rewilding principles (Carver et al., 2021) represent an ambition to shift biodiversity conservation from "Nature for people" and its concerns with ecosystem services and economic values of nature, to "People and nature" and its concerns with social-ecological systems, resilience, and adaptability (Mace, 2014). This implies a systemic transformation in current approaches to landscape management from reductive science and prescriptive policies to transdisciplinary ecological and social science, the experiential learning by stakeholders in rewilding projects, and policies that support social learning, emergence, and adaptation. The story of beaver reintroduction presented in this case and the application of principles for enhancing the resilience of ecosystem services (Biggs et al., 2012) to different aspects of beaver impacts on landscape processes, illustrate the transformational potential of beavers, rewilding principles and SES thinking to biodiversity conservation and agriculture.

Beaver dams have considerable potential as an NbS to reduce the impacts of drought by conserving water (Pilliod et al., 2018; Dittbrenner et al., 2022; Pollock et al., 2023), while their ability to reduce flooding depends on the interactions between material available for dam construction (Ronnquist and Westbrook, 2021), stream geomorphology (Larsen et al., 2021), rainfall duration, extent and intensity of rainfall and soil wetness (Breinl et al., 2021). Rainfall characteristics and soil wetness will similarly affect mechanical flood reduction measures. A study to estimate the costs and benefits of engineered versus beaver flood mitigation measures would be useful for planning future flood risk reduction measures.

An SES perspective on the contribution of beavers to the resilience of agricultural landscapes emphasizes the importance of slow changing components such as soil and hydrological systems that create stability in a landscape, and reinforcing feedback of comparatively fast changing human activity that is degrading these components. Maintaining the stability of hydrological and soil ecosystems is essential for the resilience of agriculture, especially in the face of accelerated climate change. Beavers can play a significant role in slowing the degradation process, especially if buffer zones are created between beaver inhabited streams and agricultural land. Beaver dams, wetlands and buffer zones would act as reservoirs for the biodiversity which is another key component of ecosystem resilience (Biggs et al., 2012). Unless economic policy places a limit on growth and farmers learn agroecological methods for farming with nature, climate change, soil, water, and biodiversity loss may result in the collapse of agricultural landscapes. Ecosystem renewal following collapse described in Holling's panarchy (Holling, Gundersen & Holling) are part of the evolutionary process that maintains life in a changing world and is best achieved by ensuring that the components needed for successful reorganization are conserved.

Well established beaver populations, wetlands and buffer zones provide a foundation for post-collapse recovery serving as both a natural insurance policy and a risk reduction measure. Post collapse recovery would include a transition towards agro-ecological methods of farming (Bezner Kerr et al., 2023) and the third stage of sustainable intensification (Pretty, 2018).

Scaling beaver reintroduction from enclosures and limited reintroduction sites requires a combination of learning, adaptation, and social skills for navigating the complexity of interactions between beavers and humans in a process of adaptive governance (Cosens and Gunderson, 2018) that enables beavers and human to coexist. The literature search undertaken as part of this case study found an adaptive governance framework for rewilding that was developed in the US and is consistent with much of the SES literature on adaptive governance. Studies of beaver human interactions in England, Scotland and Bavaria show how systems for adaptive governance evolved in Bavaria and are evolving in Scotland and England under the influence of Bavarian experience.

Scaling up requires the development of skills needed to navigate the social and political environment necessary to achieve changes in policy and legislation. Scaling up also requires a mindset change ("scaling deep") from the anthropocentric perspective of nature as a source of ecosystem services to an ecocentric perspective of humans and nature coexisting in an interdependent relationship sought by the rewilding principles (Carver et al., 2021). Achieving a mindset change begins at an individual level (O'Brien and Sygna, 2013; Moore et al., 2015; Amel et al., 2017) and at a societal level is a long-term process (Meadows, 2009). The slow process of mindset change is recognized in rewilding (Jepson et al., 2018; Hawkins, 2023). Rewilding principles require that people involved in planning and policy learn how to apply the social-ecological systems framework to achieve the goal of rewilding (Hawkins, 2023) as an adaptation that enhances the resilience of landscapes and to surrender the belief that living, self-organizing systems can be understood through reductive science and controlled through policy prescription.

It seems unlikely that policy support for rewilding in England will be forthcoming soon (EFRAC, 2023b) although some aspects of beaver reintroduction may be forthcoming through the ELM scheme (DEFRA, 2020).

Author contributions

MJ is the senior author, undertook the literature review and assessment of the potential of rewildling with beavers as a nature-based solution. CJ provided the story upon which the review is based and proposals for policy and practice based on his knowledge of beaver management in agricultural landscapes. All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

Author CJ co-owns the company Woodland Valley Farm.

The remaining author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Uniting hearts and lands: advancing conservation and restoration across the Yellowstone to Yukon region

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In view of the escalating anthropogenic impacts of climate change, habitat loss, and fragmentation, a broad consensus within the science community has identified large landscape conservation as critical to the future of nature and humanity. Recent commitments made at a global level offer an unprecedented opportunity for the conservation of biodiversity, particularly inasmuch as Canadian and US policies are aligned, ambitious, and clearly focused on ensuring that conservation work respects and supports the rights of Indigenous Peoples. These commitments align with and support the Yellowstone to Yukon (Y2Y) mission of connecting and protecting the 2,100-mile-long Yellowstone to Yukon region for people and nature to thrive, with the predominant approach of working with local communities and Indigenous Peoples to advance enduring conservation. Since the inception of the vision in 1993, significant progress has been made as indicated by the expansion of protected areas by more than 80 percent, the recovery of some species such as grizzly bears and wolves, and the ecological restoration of key lands across the region. While 25 percent of the Yellowstone to Yukon region is already managed or co-managed by Indigenous Peoples, today Indigenous Peoples are increasingly asserting their leadership and driving forward new restoration and conservation. New Indigenous-led conservation brings critical energy and visions that advance the Y2Y mission and arguably is a model for other parts of the world committed to achieving the 2030 UN Global Biodiversity Framework.

KEYWORDS
Canada, USA, large landscape, restoration, indigenous

Global to national policies

In December 2022, 196 countries committed to a set of ambitious targets in the Kunming-Montreal Global Biodiversity Framework (GBF) under the United Nations Convention for Biological Diversity. This mandate creates an opportunity to move the practice of biodiversity conservation and ecosystem restoration from a narrow focus on protected and conserved areas to a broader approach incorporating ecological networks that recognize and respect the rights of Indigenous and local people. While the GBF is complex with four long-term goals and 23 Targets, the following few sections are particularly relevant in this regard.

Some of the priorities particularly relevant for Y2Y region include protecting 30 percent of lands and waters by 2030 and doing so while respecting the rights of Indigenous Peoples and local communities. This is a significant step toward what nature needs, which others have identified as likely closer to 50 percent (Woodley et al., 2019).

Despite that the United States has not ratified the UN CBD global agreement, national priorities in the United States regarding nature conservation reflect those in Canada, both which align substantially with goals and targets in the GBF. As host of the December 2022 Conference of the Parties (COP) that resulted in the GBF, Canada's Prime Minister opened the conference by committing Canada to: halting and reversing the decline of biodiversity; committing to 30x30; providing up to $800 million for Indigenous-led conservation; and funding for an Indigenous Guardians network among other significant commitments that advance nature conservation and support and respect Indigenous rights (Weston and Greenfield, 2022). During the Conference, both the Yukon Territorial government and British Columbia committed to 30x30, and other provinces and territories are known to be exploring such commitments as well. Thus, goals and targets of the GBF are alignment from global to national to regional Canadian governments for nature conservation.

In the United States, the most current guiding document for nature conservation is *America the Beautiful*, an initiative released by the White House that guides efforts to restore, connect, and conserve 30 percent of lands and waters by 2030, parallel with GBF priorities. The document also ties this approach to a healthy economy as well as human health and well-being. Importantly, one of the key guiding principles in *America the Beautiful* is "honoring Tribal sovereignty and supporting the priorities of Tribal Nations," including respect and honor of sovereignty, treaty and subsistence rights and religious freedom in conservation and restoration work (USDOI et al., 2021).

The following section examines how these global and national commitments translate to on-the-ground action helping to rewild the Yellowstone to Yukon region.

Y2Y evidence of rewilding in the context of rewilding

In the early 1990s, a group of conservations and scientists set out a vision of a network of protected habitats along the spine of the Rockies, named Yellowstone to Yukon (Y2Y), that if established would allow wide-ranging species such as wolves (*Canis lupus)*, grizzly bears (*Ursus Horribilis*), and golden eagles (*Aquila crysaetos*) to thrive now and into the future (Chester 2006, Hilty and Zenkewich, 2022). Early on Y2Y was a loose coalition of conservationists and scientists interested in achieving conservation at the scale that nature needs, looking beyond individual protected areas to a connected network of protected areas. Initial efforts focused on identifying key connectivity areas and forming relationships and building trust with and among the communities living within the region, including Indigenous People (Hebblewhite et al., 2021). To date, at least 734 different entities have engaged at different times to help advance this vision (M. Strebel pers. com.). Knowledge and collaboration remain underlying tenets of how to get this work done.

As one of the earliest large landscape concepts that has been actively promoting conservation for 30 years, Y2Y is a natural laboratory to address questions about the power of a large landscape vision in advancing conservation, including rewilding. A recent analysis showed that protected areas have increased by 80 percent in the first 25 years, double the rate of protected area growth across North America as a whole (Hebblewhite et al., 2021, Figure 1). At least a quarter of all the areas protected in the Y2Y region are managed or co-managed by Indigenous People. Whereas few designated wildlife road crossing structures in the Y2Y region existed in 1993, this large landscape now encompasses at least 126 designated wildlife underpasses and overpasses and associated fencing to help keep wildlife safely connected across busy roads — more such structures than any equivalent region (Hebblewhite et al., 2021; and updated analyses). While not all busy roads have yet been mitigated, a dozen more such crossings are advancing through the planning and design phases, and wildlife infrastructure is becoming more of a standard consideration in road infrastructure (e.g., Goldfarb, 2023; Montana Fish Wildlife and Parks, 2023). Private lands and co-existence work (see Cabinet Purcell case study below) also have concretely advanced implementation of the vision and rewilding. Correspondingly, grizzly bears in the U.S. and in Alberta have measurably rebounded in population size (Hebblewhite et al., 2021). Such advancements provide early evidence that a large landscape vision can inspire local conservation that is important at a large landscape scale.

To date, conservation progress in the Y2Y region has been substantial, and recent announcements indicate that this progress is building momentum in a way that realizes Indigenous rights. The Y2Y region overlaps with at least 75 Indigenous territories of First Nations, Inuit, Métis, and Native Americans. As with non-Indigenous communities, Indigenous People tend to focus their efforts within their individual traditional territories. For example, in Canada, Indigenous leadership driving forward protected area creation has accelerated in recent decades. Two prominent examples are the 1.17 million-acre (30,050 km^2) Nahanni and the 1.19 million-acre (4,895 km^2) Nááts'įhch'oh National Park Reserves, which became co-managed by Parks Canada and First Nations in 2009 and 2012 respectfully. As Dene member, Morice [Maurice in other references] Mendo, emphasizes, the relationship between Dene People and nature is inextricably linked: "*We, the*

FIGURE 1
The fuzzy-bounded Y2Y region: an area covering 1.3 million square kilometers, stretching 3,200 kilometers north to south and 500 to 800 kilometers east to west, and spanning across five American states, two Canadian provinces, two Canadian territories, and the traditional territories of at least 75 Indigenous groups. Map showing growth of protected lands (light green) in 1993 and after 2018 (dark green) see Hebblewhite et al., (2021).

Dene people and wildlife, need the land. Without the land there is nothing to talk about" (Parks Canada, 2017).

Indigenous leadership advancing protected areas has become more widely accepted, thanks to the Canadian federal government's commitment that Indigenous leadership will guide protected area efforts (Weston and Greenfield, 2022). Since 2019, support for Indigenous conservation has resulted in signed conservation agreements between the federal, regional, and First Nations governments on approximately 14 million acres (56,656 km^2) of what will be co-managed protected areas in the Y2Y region. These include the Peel watershed land-use plan in Yukon Territory; the Peace River Caribou Agreement to restore and rewild caribou (*Rangifer tarandus)* in northeastern British Columbia (see case study below); and Qat'muk, the home of the Grizzly Bear Spirit in the upper Columbia River in southeastern British Columbia (Y2YCI, 2021). Currently, implementation of these agreements are in federal, regional, Indigenous governmental processes including on-the-ground designation.

Just in the first few months of 2023, new efforts have gained publicity and traction. For example, three Indigenous-led conservation initiatives in B.C. have been announced, resulting in the intended protection of 4.4 million acres (17,806 km^2). These include a historic implementation agreement between B.C. and the Blueberry River First Nations; a Conservancy in the Incomappleux of B.C.'s rare inland temperate rainforest in the Upper Columbia region; and the Taku River Tlingit declaration specified their plan for an Indigenous and Conserved Protected Area in the Taku River watershed. In addition, the Dene K'éh Kusān is a protected areas vision by the Kaska Dena on ancestral lands and B.C.'s largest intact landscape of 3.9 million ha (9.6 million acres; Dena Kayeh Institute undated).

In the United States, tribal leadership on both the Wind River Reservation in Wyoming as well as the Confederated Salish and Kootenai Tribes in Montana established designated tribal wilderness areas on their respective reservations, in the 1930s and 1982. Within their reservation, the Confederated Salish and Kootenai have also insisted on and led the installation of one of the most progressive sets of wildlife road-crossing structures in the United States. Phase I of this work included 41 crossing structures, including one overpass, within a 90-kilometer stretch of road, and now at least 22,000 animals use these crossings annually (Christy and DiGirolamo 2022). The tribe is now initiating the second phase of the project, starting with a major structure to be installed where at least eleven grizzly bears have been killed in the last five years (Sagner, 2023). Also, in 2020, through congressional legislation, the National Bison Range that had been previously managed by the U.S. Fish and Wildlife Service was restored to ownership and management by the Confederated Salish and Kootenai (Smith, 2022; see also https://bisonrange.org/). The tribes have already started to update the Bison Range, such as overhauling the visitor's center to reflect the tribes' languages and their relationship with bison (Monares, 2022). In Montana, the Blackfeet worked with the conservation community to retire oil and gas leases in the Badger-Two Medicine region and discussions over the last decade suggest the area may be co-managed in the future (Lundquist, 2019). While not the same level of commitment as in Canada, the U.S. federal government has signaled the importance of Indigenous leadership in conservation, which could entail increasing opportunities for Native Americans to advance their conservation visions.

Given the increasing leadership role of Indigenous Peoples, the role of conservation NGOs and other partners has shifted from leading efforts to advance protected areas to supporting Indigenous leadership and their conservation visions where these align with their organization's priorities. This means supporting Indigenous efforts by helping to secure funding, advancing collaborative science, engaging in political strategizing and communications, organizing public engagement, and more. Many of these efforts necessarily involve rewilding as so often the ecosystems and habitats in question have been subject to intensive impacts. This restoration, often done collaboratively with the support of many groups over time, helps the landscape regain functional processes ranging from natural flooding, fire, and predator-prey interactions — as well as rebalancing Indigenous Peoples' relationship with the land.

The follow section highlights several case studies that are in progress, a subset of which highlight increasing Indigenous leadership in conservation.

Case study: Peace River Break and caribou conservation

In northeastern British Columbia, where the Boreal Plains meet the Northern Boreal Mountains and the Rocky Mountain Hart Range intersects with the Peace River, lies an area referred to as the Peace River Break (PRB). The PRB is a critical pinch-point in the continuity of ecologically intact and functioning landscapes along the north-south extent of the Canadian Rocky Mountains, yet less than 4 percent of the region had been designated with protected area status (Apps C, 2013). The PRB is experiencing industrial-caused disturbances at significant rates: forest harvesting, recreation areas (including heli-ski tenures), mining, agriculture, and seismic lines directly affect approximately 27 percent of the PRB, with the result that half of the PRB is within half a kilometer of roads, reservoirs, and/or oil and gas infrastructure (Mann and Wright, 2018). Human use pressures on this landscape have placed old-forest dependent species such as caribou. This species is dependent on the food source of arboreal lichens, which in turn require large areas of continuous tracts of undisturbed alpine and subalpine parkland habitats and mid-elevation old-growth forests (Johnson et al., 2004). Central and Southern Mountain populations of caribou are endangered, with most herds at precariously low levels and in decline while others have already been extirpated from the landscape (e.g., the Burnt Pine population). Since 1920 in British Columbia alone, caribou have dropped from 40,000 to 15,000 thousand animals (Oud, 2020).

Over much of the last decade, Indigenous governments, conservation organizations, and researchers have worked together to investigate and understand the extent of impacts in the area, and to support conservation initiatives such as the successful Klinse-za Caribou maternity pen initiative led by West Moberly and Saulteau First Nations (Apps C, 2013; Burkhart, 2018; Curtis, 2018; Mann, 2020). More recently, research and knowledge gathering were used to support significant conservation responses in the area (e.g., McNay et al., 2022). The leadership of the West Moberly and the Saulteau First Nations advancing their vision of caribou recovery through federal and provincial government negotiations led to a Caribou Recovery Partnership Agreement with the federal and provincial government in 2019 (ECC Canada, 2020), which in turn resulted in the tenfold expansion of the Klinse-za Provincial Park from 2,689 ha (26 km^2) to 28,000 ha (280 km^2) in February of 2020, with a further planned expansion to 206,000 ha (2,060 km^2). These expansions are surrounded by other land use agreements focused on restoration and conservation. In addition, the Partnership Agreement includes an interim moratorium on all new tenures and development on a further 550,000 ha (5,500 km^2) of high elevation caribou recovery area (Figure 2). Although interim, it can only be lifted if all parties agree — a very unlikely proposition given the long-term caribou recovery goals of the West Moberly and Saulteau First Nations as well as Canada's commitments under the Species at Risk Act (British Columbia, undated). These new Indigenous-led conservation efforts represent an important conservation gain for both caribou and climate change resiliency within the critical ecological pinch point of the Peace River Break. However, much work remains in rewilding this heavily disturbed landscape.

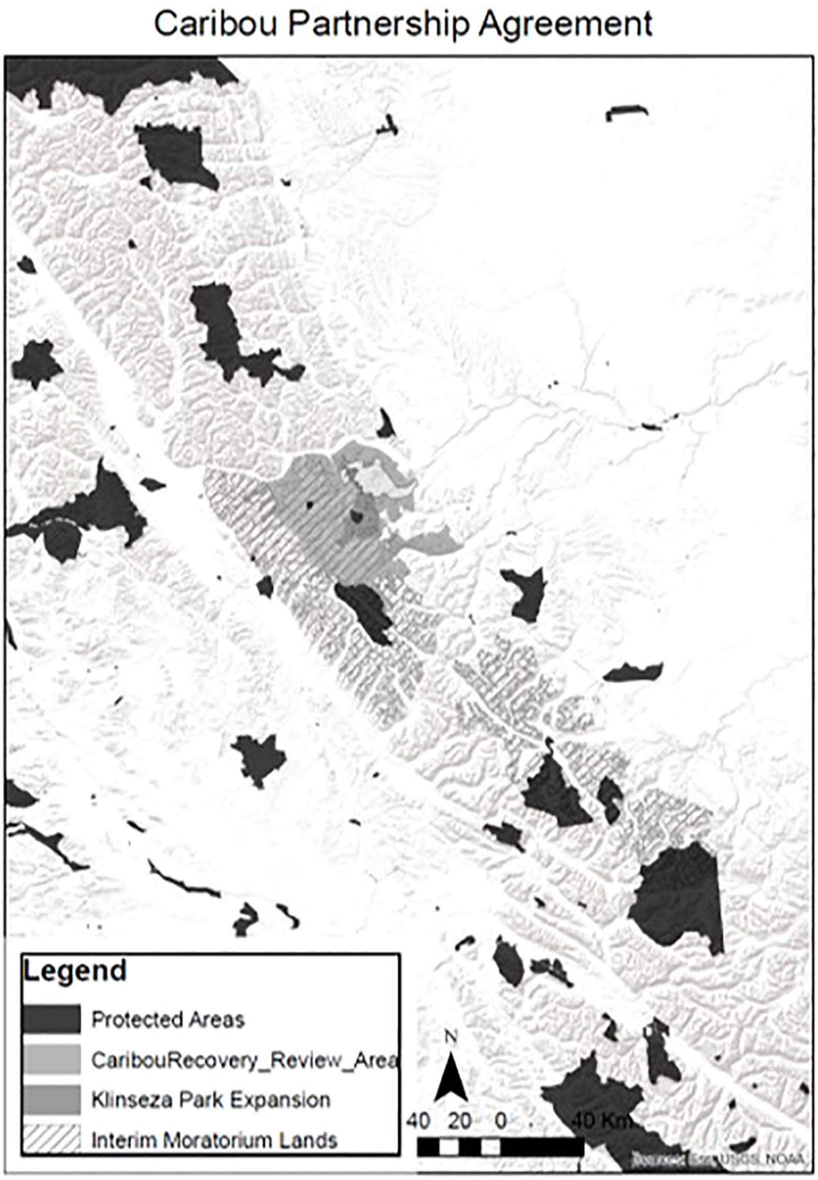

FIGURE 2
A map showing the conservation gains from the Peace River region Caribou Agreement, a signed agreement between the West Moberly and Saulteau First Nations and the British Columbia and Canadian federal government.

Case study: large carnivore rewilding in the southern region of Y2Y

During the inception of the Y2Y vision in the mid-1990s, many of the individuals at the founding meetings were concerned with the already extensive range loss across North America for both large carnivores as well as hooved animals (Harvey, 1998). As a mapping exercise by Laliberte and Ripple (2004) demonstrated, one of the last places where most of these animals still roam is within the Y2Y region.

Worldwide, applied research has increasingly shown that the loss of large predators leads to a cascade of ecological impacts affecting multiple parts of ecosystems (Smith et al., 2020). As one of the more well-studied ecosystems in the world, the Greater Yellowstone Area has been a *de facto* natural laboratory for a plethora of research on such trophic cascades. Specifically, due to the extinction of several large carnivores from all or parts of the ecosystem in the early 1900s and the subsequent restoration or rewilding of carnivores back into the system, researchers have been able to understand the role of carnivores by examining differences before and after their restoration.

The body of studies on the pre- and post-restoration of large carnivores in the Greater Yellowstone Ecosystem has covered a diversity of species and topics. While grizzly bears never completely disappeared from the Greater Yellowstone region, fewer than 150 were thought to persist by the 1970s (USNPS, 2020a). Following complete extirpation, wolves were reintroduced as an experimental population to Yellowstone in 1995. Mountain lions (*Felis concolor*) and wolverines (*Gulo gulo*) were generally assessed as extirpated from the area, and genetics studies suggest that they naturally returned from more northern Canadian populations in the late 20th and into the 21st century (Yellowstone Science, 1994; McKelvey et al., 2014).

Studies of these animal recoveries have shown dramatic effects. For example, the expansion of grizzly bears back to Grand Teton National Park has led to the restoration of willows and an increase in the associated bird communities, as well as a shift in the age structure of a once senescing moose (*Alces alces*) population (Berger et al., 2001). Large carnivores can both reduce hooved animal populations and change their behavior — such as where they spend time in the landscape — resulting in a cascade of impacts in the ecosystem. Ongoing research details how the restoration of wolves has played an enormous role in shaping ecosystems, ranging from changing riparian vegetation and hydrological processes to altering the abundance of many different species across the park. Notably, the impacts and results are varied across the park where wolves now roam. As one of the world's most well-studied reintroductions, the findings of wolf reintroduction to Yellowstone offer lessons too numerous to expand on here, but overall the preponderance of evidence supports that the suite of large carnivore species that are now restored to Greater Yellowstone play a significant role in shaping the ecosystem itself (Smith et al. (2020) stands out amongst the myriad accounts of Yellowstone wolf reintroduction). Lesser known but also important was the wolf reintroduction to the Idaho wildlands complex by the Nez Perce at approximately the same time. The Nez Perce exercised their Treaty rights reintroducing wolves despite the misgivings of the state of Idaho. This wolf population continues to thrive although, like Yellowstone, management of the population continues to be politically controversial (Nez Perce Wildlife Division, undated).

The phenomenon of trophic cascades carries important implications for the Y2Y vision across the Y2Y region. With large carnivores absent or in low numbers in other parts of the Y2Y region, including the extensive Idaho wildlands complex where grizzly bear populations were exterminated in 1940s, restoring the full complement of carnivores to such large wild regions will also help to restore and maintain healthy ecosystems. In addition, scientific research indicate that maintaining such species in any part of Y2Y in isolation can be highly problematic since the habitat requirements of a viable long-term population often span beyond any individual subregion of Y2Y. Science has clearly demonstrated that even large ecosystems such as the Greater Yellowstone Ecosystem and the Idaho Wildlands complex are too small to sustain some large carnivores, and thus restoring connectivity between these wild regions is also a priority. Efforts by many different non-profits and government agencies have been ongoing for decades in a race against an onslaught of human development, thus keeping the opportunity for population connectivity open. As a consequence, Yellowstone grizzly bears are closer than ever to reconnecting with their northern relatives (Montana Fish Wildlife and Park Undated).

Case study: restoration of habitat and wildlife from the Transboundary Cabinet Purcell Mountain Region to Camas to Condors Corridor through collaboratives in the Pacific Northwest

The Cabinet Purcell Mountain Corridor Project is illustrative of how many partners, including government agencies, working on a shared goal can make significant progress (Proctor et al., 2018). In the early 1990s, the population of grizzly bears in the transboundary Cabinet Purcell Mountain region of Montana, Idaho and British Columbia was showing signs of isolating into smaller populations, with one group as low as 10 individuals in Montana's Cabinet Yaak Mountains. Grizzly bear science helped to prioritize where key core habitat and connectivity zones should be protected and restored. On the U.S. side, more than 1295 km^2 (129,500 ha.) of habitat were secured through road removal projects on U.S. Forest Service land. Ensuring connectivity among the remaining bear populations required securing private land through conservation easements and acquisitions, which significantly increased the security of three identified corridors.

Additionally, the state of Idaho purchased one priority corridor to be restored as a Wildlife Management Area, where the focus was both on restoring wetlands for endemic wildlife such as native bees, native toads and frogs, and other wildlife, as well as on increasing connectivity across the broader landscape for bears and other large mammals (https://idfg.idaho.gov/bees2bears; Figure 3). More than 20,000 shrubs and trees were planted in recontoured wetlands to help rewild a climate resilient landscape, and a grizzly bear print was found amidst the restoration during the summer of 2020 (J. Grossman, pers. com.). Other key efforts in the region to support grizzly bear restoration have included the installation of more than 170 electric fences to deter bears from attractants such as bee hives, chicken coops, and fruit orchards, educational efforts on preventing human-wildlife conflict, and other projects. With these efforts having built on several decades of work to increase grizzly bear connectivity in the area, recent research on tracked movements between the previously isolated populations and beyond those populations indicates that conservation efforts have already had an impact (Proctor et al., 2018; Hilty et al., 2019). Likewise, the Cabinet Yaak populations of grizzlies increased to over 60 individuals through the work of more than 50 entities in the collaboration.

The Nez Perce Tribe, which engaged in the Cabinet Purcell partnership, are today leading the Camas to Condors Corridor Project (NPTWRD, 2019). Modeled to a degree on the Cabinet Purcell partnership, this initiative entails landscape-level planning efforts by the Tribe in partnership with University of Idaho and non-profit partners that seek connectivity for wildlife and the restoration of cultural relationships with nature. The Camas to Condors project is based on the understanding that nature and people are inextricably linked, with, for example, the Nez Perce's

FIGURE 3
A grizzly bear footprint remains in the sun-baked mud in the area of the bees to bears project, a wetland corridor restored in the northern Idaho panhandle to reconnect grizzly bears and help other wetland wildlife with a climate adaptation restoration project.

tending of camas (*Camassia*) helping the plant flourish and remain healthy, producing bulbs that fed not only the Nez Perce but also grizzly bears and other wildlife. One important aspect of this project is restoring connectivity between Nez Perce people, plants, and animals across the landscape. While this is a huge vision, the Nez Perce understand that it is about building on projects over time and starting and engaging in projects that invite in partners to help these projects advance and support the vision.

Case study: bison restoration

Bison (*Bison bison*) are a megaherbivore keystone species that literally shape the ecosystem they occupy. While the history of their collapse across North America is generally well-known, their current status and conservation challenges today are perhaps more complex and less understood by most of the public. Bison flourished across North America until the time of European invasion and the associated slaughter of bison that nearly drove them to extinction in the late 19th century (Sanderson et al., 2008). In 1905 when a few key individuals realized that bison were on the brink of extinction, they formed the American Bison Society to restore the species in various localities across North America. By the 1930s, about 20,000 bison had been restored in various conservation herds, a number similar to today (although approximately 500,000 bison are now found in "ranch" bison that were often cross-bred with cattle). What is less well known is that in some arenas, bison have been and remain anathema — so much so that their status as "wildlife" has been threatened, and many states and provinces still recognize bison as solely livestock (or in some cases, as livestock as well as wildlife). The result is that unlike any other wildlife in the Y2Y region, bison are subject to the unique restriction of confinement to particular areas within their range. They face an additional challenge of various levels of genetic heritage, with ranchers having long sought to interbreed bison and cows to obtain a more hardy but easy to manage animal. Additionally, some conservation herds are small populations that must be managed for inbreeding. A further challenge is that some populations of bison have acquired diseases transmitted from cattle, most notably brucellosis in the Greater Yellowstone Ecosystem. The presence of disease presents challenges to relocating bison or allowing bison to roam and mix with cattle due to concerns over disease transmission back to now disease-free cattle (White et al., 2011).

These circumstances meant that for most of the latter half of the 20th century, the population status of bison conservation herds changed little (~20,000 bison), while bison ranching expanded enormously. In the late 20th century, conservationists re-awakened to the plight of bison conservation, taking a fresh look at where restoration of bison at scale could occur in key locations across North America (Sanderson et al., 2008). Three key places where bison restoration is advancing today are in the Y2Y region. The first is on the northern and western edges of Yellowstone National Park, a region where bison leaving Yellowstone National Park were once hazed back into the park or shot. Due to work of various entities, the state of Montana has created a buffer zone that allows bison to leave the park within these defined spaces. However, they are still limited in their movements outside the park, and Yellowstone bison are still slaughtered when their numbers are deemed too high to be supported by the habitats they are allowed to access (White et al., 2011; National Park Service, 2018). All the same tribes that have treaty rights to hunt these bison, such as the Nez Perce, as well as non-tribal members, have established limited bison hunts outside of park boundaries.

In 2017, an experimental population of bison was restored to the northern reaches of Canada's Banff National Park, with an initial soft release of 16 bison. Now there are approximately 80 bison that roam freely in the park (Parks Canada, 2022). However, like the situation in Montana and Yellowstone, the confines of jurisdictions that "allow" for wild bison are still restrictive in Alberta, and these bison are prevented from leaving the park. Although the Alberta government has created a buffer zone on adjacent non-park public lands, bison are still considered livestock beyond that buffer and currently cannot roam further — although many in the conservation community hope that this will change with time. Likewise, it is unclear how the relationship between this recovering herd and the area's Indigenous Peoples will develop. As both have deep, intermingled historical roots in this region, this relationship needs to be addressed in the near future.

Another inspiring rewilding bison project is envisioned by the Blackfoot Confederacy, a transboundary group of Indigenous Peoples living along the Montana-Alberta border who have been advancing the Iinnii Initiative since 2009. This effort seeks to conserve traditional lands, maintain Blackfeet culture, and enable bison, or Iinnii in Blackfeet language, to return to their lands (Blackfoot Nation, 2020). Recognizing that both people and bison are split by political boundaries, this initiative seeks a holistic approach to the restoration of lands, wildlife, and people (Blackfoot Nation, 2020). In June 2023, more than 40 bison were released to be free-roaming in the Chief Mountain area east of Glacier National Park (Scott, 2023). Someday in the not-too-distant future, bison may once again roam across broader Blackfoot Confederacy territorial lands, including in Canada and the United States and adjacent national parks such as Glacier and Waterton, and perhaps other jurisdictions.

Next steps

The vision for the Y2Y region is to connect, restore and protect the region so that both people and nature can thrive, and accomplishing it means both protecting extant nature as well as the rewilding and restoration of key ecosystems and species and maintaining and restoring human connectivity with nature. Today this work will be driven by community-level priorities although such efforts could be accelerated by higher-level enabling policies that better recognize and support large landscape conservation. Indigenous leaders are increasingly leading the call for new protected areas and, in some cases, also advancing connectivity conservation across their traditional territories. In Canada, there is unprecedented support for such Indigenous leadership. The approach of conservation NGOs and other entities are shifting to supporting Indigenous visions that align with their own organizations' missions. This work requires developing relationships, understanding where and how partnerships can be helpful, and moving both at the speed of trust as well as the capacity of communities.

While substantial and important rewilding is continuing to advance in the Y2Y region, there are still considerable ongoing challenges for conservation. Mountain caribou (*Rangifer tarandus caribou*) are found nowhere else on the planet except in the Y2Y region. In 2018, the loss of a transboundary herd between the U.S. and Canada meant there are no longer caribou in the lower 48 states. Many other populations of mountain caribou are suffering major declines in populations. While the Caribou Recovery Partnership Agreement in B.C.'s Peace River Region is a model for advancing their recovery, a challenge is to advance similar measures across the mountain caribou range. Many Indigenous communities are advocating for recovery of caribou as a culturally important species (e.g., Fraser Basin Council, 2023), so perhaps with their leadership and engagement we can see the revival of caribou populations and other species across the Y2Y region in the future.

Likewise, although ecosystem fragmentation from the human footprint of built infrastructure and the linear disturbances of roads and other corridors are the single biggest threat to ecological values, the human footprint from recreational use is an increasing issue (Larson et al., 2016; Vilalta Capdevila et al., 2022). The need to understand the cumulative impacts of development as well as increasing human activities is yet another challenge on this landscape. As these challenges increasingly fill the spaces between and around (and sometimes within) protected areas, they ultimately affect our capacity to achieve large landscape conservation instead of islands of conservation. We also need to continue to expand conservation to be more intersectional in addressing these challenges. This means not only engaging with western science, but also Indigenous and local knowledge, braiding together multiple ways of knowing to strengthen our collective approach to advance conservation.

Summary

The essence of rewilding remains core to advancing conservation in the Y2Y region. We also know that conservation of carnivores, core areas, and corridors requires engagement and commitment by people. Indigenous communities and governments across the region have been and increasingly continue to lead the way in connecting people to land and wildlife. Such projects restore and maintain a vital cultural value at a time where world and national commitments in North America are ambitious and aligned with many Indigenous People's vision for their lands. It is only if humanity invests in nature as the highest and greatest good in North America's most intact large mountain region, Y2Y (Theobald et al. accepted), that we will be able to maintain and restore both biodiversity and culture in this region.

Author contributions

JH: Conceptualization, Investigation, Project administration, Supervision, Writing – original draft, Writing – review & editing. CC: Conceptualization, Formal Analysis, Writing – original draft, Writing – review & editing. PW: Conceptualization, Formal Analysis, Writing – original draft, Writing – review & editing. KZ: Conceptualization, Formal Analysis, Writing – original draft, Writing – review & editing.

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Rewilding landscapes with apex predators: cheetah (*Acinonyx jubatus*) movements reveal the importance of environmental and individual contexts

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Rewilding landscapes through species or population restoration is an increasingly applied practice in biological conservation. There is expanding interest in wildlife release projects for apex predator population augmentation or reintroductions in historical ranges. Cheetahs (*Acinonyx jubatus*) are an IUCN Vulnerable-listed species with a declining global population facing major threats, which in southern Africa primarily include lethal persecution on livestock farms and bush encroachment transforming open habitats to woody areas. We used GPS radiocollars to monitor ten adult cheetahs from 2007 – 2018 in the Central Plateau of Namibia encompassing an area restored as an open savanna field (13.7 km^2) located in a matrix of woodland savanna affected by bush encroachment. We generated a set of a priori hypotheses that tested the effects of various factors on cheetah movements indexed by step length. We compared cheetah movement metrics based on their history as wild, rehabilitated, and/or translocated individuals. Day/night activity, habitat type, and habitat edges were significant predictors of cheetah movement. Wild resident cheetahs displayed significantly longer steps than the other cheetah classes, possibly suggesting increased territorial behaviour in response to the presence of introduced cheetahs. Some cheetahs temporally segregated by moving extensively during daytime, but most individuals were primarily active during crepuscular periods. Small prey remained constant across time, whereas large prey declined over the study period. Cheetahs appeared to adjust behaviourally by increasing movements in years when large prey were scarce. Cheetahs appeared to be ecologically adaptable and behaviourally flexible in response to varying prey populations and when translocated to new environments, specifically at the interface between bush-encroached woodland and open savanna. Environmental settings and animal history need to be carefully considered in rewilding and ecosystem restoration, and monitoring of released and resident individuals, if present, is important to understand ecological dynamics at release sites.

KEYWORDS

behavioural adjustments, bush encroachment, ecosystem restoration, large carnivore, movement ecology, restoration ecology, translocation, wildlife rehabilitation

1 Introduction

Habitat loss, illegal killing, declining prey, and human-wildlife conflicts threaten the survival of apex predators globally (Woodroffe, 2006; Ripple et al., 2014; Lennox et al., 2022). Terrestrial apex predators confront challenges that extend beyond ecological realms, impacting economic and political dimensions of conservation (Jhala et al., 2020). In Africa, many large carnivores are classified by IUCN as endangered (e.g., the Ethiopian wolf [*Canis simensis*] and African wild dog [*Lycaon pictus*] or vulnerable (e.g., cheetahs [*Acinonyx jubatus*], lions [*Panthera leo*]), requiring conservation action for persistence or recovery (Durant et al., 2017; Marneweck et al., 2019; Seid et al., 2022).

Cheetahs face alarming population fragmentation and decline, with an approximate count of 7,100 adults and subadults remaining across Africa predominantly outside protected areas (Durant et al., 2017; Marker et al., 2018a). While we cumulatively know much about baseline cheetah ecology (Caro, 1994; Durant et al., 2007; Marker et al., 2018b), information on cheetah movement ecology is sparse. Insights from movement analysis of carnivores hold the potential to inform human-wildlife conflict mitigation and bolster critical ecosystem services by maintaining carnivores on the landscape (Odden et al., 2014; Van der Weyde et al., 2017; Loveridge et al., 2022; Teichman et al., 2023).

The world's primary cheetah population stronghold is in southern Africa (Durant et al., 2017; Marker et al., 2018a), but cheetahs therein are subject to lethal persecution on livestock farms and in many areas must contend with bush encroachment, which can alter both predator and prey behaviours (Marker and Dickman, 2004; Nghikembua et al., 2021; Atkinson et al., 2022a; Nghikembua et al., 2023). Habitat change to woody vegetation potentially affects the cheetah's hunting strategies and energy acquisition, given their preference for open landscapes (Caro, 1994; Atkinson et al., 2022b). While both human-wildlife conflict and habitat change can be tackled with management and education, in some areas the cheetah populations are low or extinct, and restoration requires translocations for population recovery. In such contexts, rewilding provides a pathway to restore populations that underwent extinction or significant declines (Fritts et al., 1997; Hayward et al., 2007; Jhala et al., 2021). Human interventions involving translocation, rehabilitation, and reintroduction are instrumental in this endeavour (Odden et al., 2014; Naha et al., 2021; Walker et al., 2022).

We assessed potential differences in movement patterns and ecological correlates associated with movement, comparing wild cheetahs and those subjected to human intervention through translocation and/or rehabilitation. Understanding movement characteristics and variability according to cheetah history and

TABLE 1 Definition of the four cheetah classes in the study.

Class	Description
Wild Local	• Local to the area of CCF property. • Individuals that were not captive raised, but were collared for research purposes and released at capture site.
Rehabilitated Local	• Local to the area of CCF property. • Individuals were taken into captivity temporarily due to injury or being orphaned. • If injured, this was caused by intraspecific competition, interspecific competition (leopards), or from human-wildlife conflict. • If orphaned, tracked mother had been killed in human-wildlife conflict, or cubs were attempted to be smuggled.
Rehabilitated Translocated	• Not local to the area of CCF property. • Individuals that were taken into captivity due to injury or being orphaned, or were born in captivity. • If injured, this was caused by intraspecific competition (other cheetahs), interspecific competition (leopards, lions, hyenas), or from non-fatal human-wildlife conflict. • If orphaned, tracked mother had died due to human-wildlife conflict or died due to natural causes, or cubs were attempted to be smuggled. • Translocated to CCF property from farms where captured in human-wildlife conflict incidents.
Wild Rehabilitated Translocated	• Translocated from farms where they were captured in human-wildlife conflict incidents. • Not captive raised, but entered captivity temporarily due to injury.

Rehabilitated individuals were those that were either placed temporarily into captivity at a young age when acquired as cubs, or received veterinary care due to injury. Local individuals were those born in or nearby to CCF property, whereas translocated animals were moved from their home location to CCF property. Wild individuals had minimal human contact and were not placed into temporary captivity.

human-mediated management can assist conservation strategies and apex predator population management on African landscapes (Marker et al., 2018a; Fabiano et al., 2020). When linked to habitat conditions and prey information, apex predator movement data can allow insights into connectivity considerations and predator-prey dynamics respectively (Broekhuis et al., 2021; Loveridge et al., 2022).

Using GPS radiocollar data on cheetahs and prey information spanning 15 years, we studied movement rate (i.e., step length) (Turchin, 1998; Thurfjell et al., 2014), investigated relationships between multiple variables and movement, and examined associations with prey availability (Broekhuis et al., 2019, Broekhuis et al., 2021; Rodriguez-Recio et al., 2022) in a period with declining prey (Bandyopadhyay et al., submitted). Our cheetah data were categorised among four different classes (Wild Local, Rehabilitated Local, Rehabilitated Translocated, and Wild Rehabilitated Translocated; for full description, see Table 1). We tested the following hypotheses:

1. Cheetah movement patterns differ between individuals according to history and human intervention. Wild local individuals would move slower than translocated cheetahs due to greater familiarity with their surroundings requiring less energy expenditure. Translocated individuals are unlikely to possess the same ecological knowledge of the area, and we expected them to exhibit longer movements associated with exploratory behaviour (Walker et al., 2022).
2. Marking trees and waterholes significantly influence cheetah movement patterns as exhibited by shorter movements when in the vicinity of these landscape features. Cheetahs may claim these key resources with territorial exclusivity (Marker-Kraus and Kraus, 1997), wherein marking trees are used to advertise presence to territory contesters, and waterholes are prime hunting areas with predictable prey presence (Nghikembua et al., 2016; Broekhuis et al., 2021).
3. Cheetahs will move greater distances over time to encounter prey due to a steep decline in prey density (Bandyopadhyay et al., submitted). Although this process may also be influenced by interspecific competition and changes in habitat quality, this will not be tested in this study.
4. Cheetahs exhibit more diurnal activity than nocturnality, as a mechanism to temporal segregate from other, dominant large carnivores (leopard [*Panthera pardus*] in our system) and to maximise visibility during prey pursuits (Hayward and Slotow, 2009).

2 Materials and methods

2.1 Study area

The study took place in the Central Plateau of Namibia on farmlands that are Cheetah Conservation Fund (CCF) property. The property covers 577 km^2 and is managed as a wildlife reserve as well as mixed-use land for wildlife and livestock. The area has an average temperature of 19.2°C (+/- 2.4°C) and an annual rainfall of 400-450 mm (Marker et al., 2008). The predominant habitat type is semi-arid thornbush woodland savannah (Marker et al., 2008; Nghikembua et al., 2021), with dominant tree genera including: *Boscia, Combretum, Dichrostachys, Grewia, Senegalia, Terminalia*, and *Vachellia* (Nghikembua et al., 2021; Bandyopadhyay et al., submitted).

The focal study site for analysis centred around the 'Big Field' section of the broader property and is operated exclusively as a wildlife reserve (Lat -20.4839°, Long 17.0317°; Figure 1). 'Big Field'

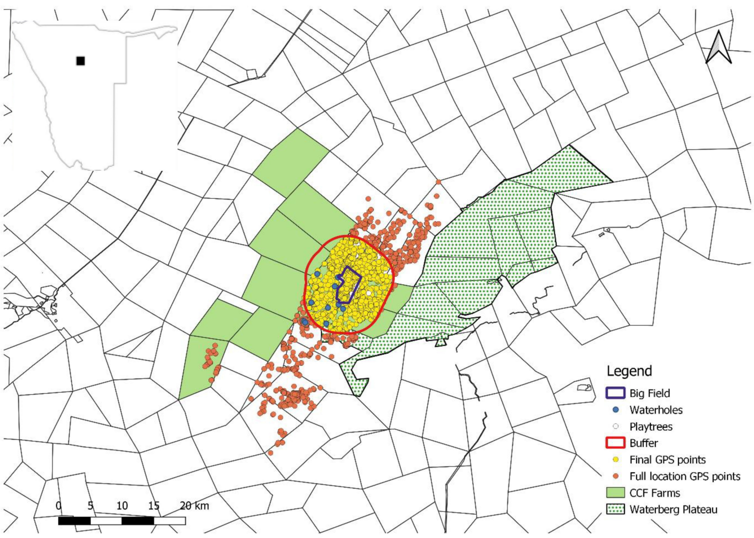

FIGURE 1
Map showing the location of the focal study area (red) in the broader landscape of North-central Namibia. The area included a large field (Big Field) managed as open savanna in a matrix of bush encroached woodland savanna. Yellow points are the cheetah GPS radiocollar locations included in the analysis.

is managed as an open savanna area covering approximately 13.7 km^2, while the remaining property is woodland savanna that is heavily bush-encroached, with bush cover >90% in some areas (Nghikembua et al., 2016). Big Field is of significant relevance as one of the largest open areas in north-central Namibia within a predominantly bush-encroached landscape.

2.2 Data collection

Cheetah data were collected via GPS radiocollars (Sirtrack – Havelock North, New Zealand, ATS – Minnesota, USA, or AWT – Pretoria, South Africa) on 17 adult cheetahs (11 females and 6 males) that were either captured on site by CCF for research and released at the capture location, or were captured on other properties by private farmers and translocated and released on the CCF property as part of human-wildlife conflict mitigation at the origin site, and cheetah population recovery at CCF. Cheetahs were captured by CCF or farmers through human-wildlife conflicts using double door (walk-through) cage traps, often at preferential cheetah marking sites. Cheetahs were anaesthetised with drug combinations including Telazol®, Ketamine-Medetomidine, or Ketamine-Midazolam (Marker et al., 2008). The capture and handling of animals adhered to approved procedures and were conducted in compliance with relevant regulations and permits (NCRST AN202101032). Additionally, some animals arrived at CCF as orphan cubs from human-wildlife conflict of livestock farms and were held in captivity in large enclosures on CCF property as part of a rehabilitation and release programme (Walker et al., 2022). All cheetahs were adult at the time of collaring and monitoring.

The available GPS location data covered the period September 2007 to May 2022, and included cheetah ID, individual history, sex, age class, reproductive class (solitary male, coalition male, solitary female, female with cubs), type of collar used, date and timestamp for each GPS location, latitude, longitude, release date, and release location.

Prey data were collected in the same timeframe as the cheetah collar data via road transects that were repeatedly driven to record ungulate observations visually. We classified prey into small (common duiker [*Sylvicapra grimmia*], dik-dik [*Madoqua kirkii*], springbok [*Antidorcas marsupialis*], steenbok [*Raphicerus campestris*]) and large categories (eland [*Taurotragus oryx*], greater kudu [*Tragelaphus strepsiceros*], oryx [*Oryx gazella*], red hartebeest [*Alcelaphus buselaphus*]).

Transects covered the entire CCF property and no habitat stratification was applied as the property can be classified as woodland savanna (Bandyopadhyay et al., submitted; Supplementary Table S1). Prey data were also collected along dedicated short transects in the Big Field section. Transects were driven at a speed of maximum 20 km/h and whenever an animal was detected, the vehicle was stopped and observers recorded the perpendicular distance from the transect to the animal for subsequent analysis in a distance sampling framework (Buckland et al., 2001). The total annual transect sampling effort was 2,382 km.

2.3 Data processing

Prior to computing movement metrics, we refined the cheetah GPS radiocollar data to focus on Big Field and a buffer region around it. GPS fix acquisition rates for the deployed collars varied along the 15-year dataset. We inspected the data and found that 3-hour fix rates were used most extensively, therefore we constrained our analysis to this fix rate. While this refinement resulted in dropping seven individuals which either had different fix rates or sparse data, using variable fix rate would have affected our inferences on animal movements from collar data (Cristescu et al., 2015). Our final sample size was ten cheetahs (weight range at release – 25 to 57 kg) across four distinct classes: Wild Local,

TABLE 2 Final data of 4,965 GPS points used to investigate factors associated with movement in a GLM analytical framework.

Class	Sex	Unique cheetah ID	Range of data collection	Number of fixes
Wild Local	Male	AJU1533	Sep 2007 – May 2008	1,529
		AJU1543	Aug – Nov 2009	120
Rehabilitated Local	Female	AJU1666	Mar 2018	66
	Male	AJU1664	Mar – May 2018	120
Rehabilitated Translocated	Female	AJU1510	Dec 2013 – Feb 2014	378
		AJU1512	Dec 2013 – Sep 2014	411
		AJU1608	Aug 2014	30
		AJU1615	Apr – Jul 2014	479
		AJU1619	Jun 2014 – Feb 2016	1,401
Wild Rehabilitated Translocated	Female	AJU1606	Mar – Jul 2011	431
Total				**4,965**

Rehabilitated individuals were either temporarily placed into captivity at a young age due to being orphans, or as older individuals due to injury necessitating veterinary care. Local individuals were those born in or nearby to CCF property, whereas translocated cheetahs were moved to CCF property from farms of origin where they were captured in human-wildlife conflict incidents. Wild individuals are those that had minimal human contact and did not experience captivity.

Rehabilitated Local, Rehabilitated Translocated, and Wild Rehabilitated Translocated, which contributed 4,965 data points for the analysis during 2007 – 2018 (Tables 1, 2). We calculated step length (movement rate) for all ten cheetahs and established the buffer size around Big Field as the 95th percentile of step length of the ten individuals pooled.

For each cheetah step we calculated distances to the closest marking tree (known from long-term monitoring to be used by cheetahs for marking), waterhole, and habitat edge of the open savanna (Big Field)-woodland savanna interface, using the distance matrix function in Q-GIS. We defined day/night cycles for each season (Cold-Dry [May-August], Hot-Dry [September-December] and Hot-Wet [January-April]; Nghikembua et al., 2021), assigning day, night or crepuscular period for each GPS radiocollar point from automated time zones (NST) using the 'suncalc' package in R (Core Team, 2021). We categorised steps as intersecting habitat edge (open savanna-woodland savanna interface), inside Big Field, or outside Big Field.

We estimated prey encounter likelihood separately for small and large prey, using the effective strip width model (ESW) and prey density estimates in a distance sampling framework (Bandyopadhyay et al., submitted). We further categorised prey by foraging strategy (browsers, grazers, and mixed feeders) when calculating prey encounter rate. Because the number of prey observations along the Big Field transects was too small to derive density estimates, we combined these monthly collected data with annual CCF property-wide transects to obtain density estimates. The property-wide estimates also had few observations of prey, therefore similarly to Bandyopadhyay et al. (submitted), we pooled the data into four-year intervals (2009-2012, 2013-2016, and 2017-2020) to relate to daily distance moved by cheetahs stratified by the same intervals. One cheetah (AJU1533) with data points in 2007 and 2008 was excluded from the predator-prey analysis due to a lack of yearly prey data for 2007-2008, attributed to staffing constraints.

Environmental influences on the cheetahs' movements other than those tested in our analyses were minimised because GPS radiocollar locations occurred in the same land use type (wildlife reserve) and the same rainfall class as derived from the Atlas of Namibia (https://atlasofnamibia.online/).

2.4 Data analysis

Step length and turning angles for the collared cheetahs were calculated using the 'move' package in R (v4.2.4) (Turchin, 1998; Thurfjell et al., 2014; Core Team, 2021). We used ANOVA, t-tests and post-hoc Tukey tests to check for significant differences in step length among class, sex, and season.

We used a Generalised Linear Model (GLM) approach with covariate combinations to determine associations of ecological factors and cheetah step length. We ran a correlation analysis to identify covariates that might induce multicollinearity, and covariate combinations with $|r| > 0.6$ were excluded from the same model structure (Supplementary Table S2). For each of the four cheetah classes, we used the same candidate model set to identify fixed-effects covariates associated with step length as the dependent variable (Table 3). We excluded prey density from the GLMs because prey density was a non-spatial estimate. For each cheetah class, we ranked models in the candidate set using the Akaike Information Criterion (AIC) corrected for small sample sizes (AICc), and considered models to be supported if their ΔAICc <2. Additionally, we ran two sets of mixed-effects models with the same fixed-effects covariates, using cheetah class and individual cheetah ID respectively as random intercepts. We ranked models in these two sets using AIC (Supplementary Tables S11 – S16).

TABLE 3 Table of multiple hypotheses tested with GLM models to investigate factors associated with cheetah movements.

Hypotheses	Covariates included	Model name	Rationale
1	Intersection + Waterhole + Edge + Edge^2 + Time of day	Global Model (no marking tree)	Exploring potential influences on movement decisions
2	Null	No Covariates	Baseline reference for comparison
3	Waterhole + Time of day	Hunting Habitat	Investigating waterhole as a key resource
4	Marking tree + Time of day	Territoriality	Examining the role of marking trees in defining territories
5	Edge + Edge^2 + Time of day	Hunting Habitat edge	Analysing movement decisions along habitat edges
6	Intersection + Time of day	Habitat Use	Assessing how intersections affect movement choices and differences in step length
7	Waterhole + Marking tree + Time of day	Resource Utilisation	Studying the relationship between movement and resource utilisation
8	Waterhole + Marking tree + Intersection + Time of day	Global model (no edge) - Resource Movement	Comprehensive understanding of resource-driven movement
9	Edge + Edge^2 + Waterhole + Time of day	Hunting Behaviour	Exploring movement patterns relating to hunting

We analysed the variability in prey density over time using Wilcoxon-tests separately for large and small prey. We contrasted the empirical prey estimates with symmetrical distributions to independently test if prey density fluctuated significantly from 2009 to 2020, using the 4-year intervals mentioned above. Finally, we determined the prey encounter rates by dividing the encounter rate per day per prey species by the total number of independent observations made during the effort. Results were split into prey foraging categories (browsers, grazers, and mixed feeders). We then contrasted them with the daily distance travelled by each cheetah class.

We used Q-GIS (v3.2.8), ArcGIS (v10.8.2), R Studio (v4.2.1) and R packages *dplyr*, *lubridate*, *suncalc*, *move*, *lme4*, and *ggplot2* for analyses.

3 Results

3.1 Movement metrics

Wild Local cheetahs had the highest average step length (1,164 m), followed by Rehabilitated Local (601 m), with both local groups displaying longer movements than Rehabilitated Translocated and Wild Rehabilitated Translocated (400 m and 278 m respectively) (Figure 2). The difference was statistically significant for Wild Local compared to all other classes (p <0.05) (Supplementary Table S3).

Cheetahs moved the shortest distances in the Cold-Dry season (405 m) compared to Hot-Dry (675 m) and Hot-Wet (632 m) periods (p <0.05) (Supplementary Table S4). Males (903 m) exhibited longer step lengths on average than females (364 m) (p <0.001) (Supplementary Table S5).

Cheetahs mostly moved in the buffer outside of the Big Field (proportion of steps 0.80) but when therein they took shorter steps (488 m). While spending less time inside Big Field, they moved faster in the open area (799 m). In contrast, steps intersecting the open savanna-woodland savanna habitat edge produced long-range movements (1618 m), but these steps were proportionally lowest compared to steps within and outside Big Field (Supplementary Table S6).

All analyses found the day, night, and crepuscular covariates to be significant, but for the mixed-effects models using pooled data, no other fixed-effects covariates were significant (Supplementary Tables S11 – S16). Cheetahs did not show a specific preference for directionality, with turning angles appearing relatively evenly distributed (Supplementary Figure S1).

3.2 Factors associated with movements

3.2.1 Wild Local

Only the Global Model (no marking tree) was supported for Wild Local individuals (Table 4; Supplementary Table S7). Wild Local cheetahs moved shorter distances during the day and night compared to crepuscular periods, and steps that intersected habitat edge were longer compared to steps inside Big Field.

3.2.2 Rehabilitated local

Four models were supported (ΔAICc <2): Global Model 2 (Resource Movement), Habitat Use model, Hunting Habitat model, and Global Model (No marking tree), but the Resource Movement model received the most support (Table 4; Supplementary Table S8). Rehabilitated Local cheetahs moved

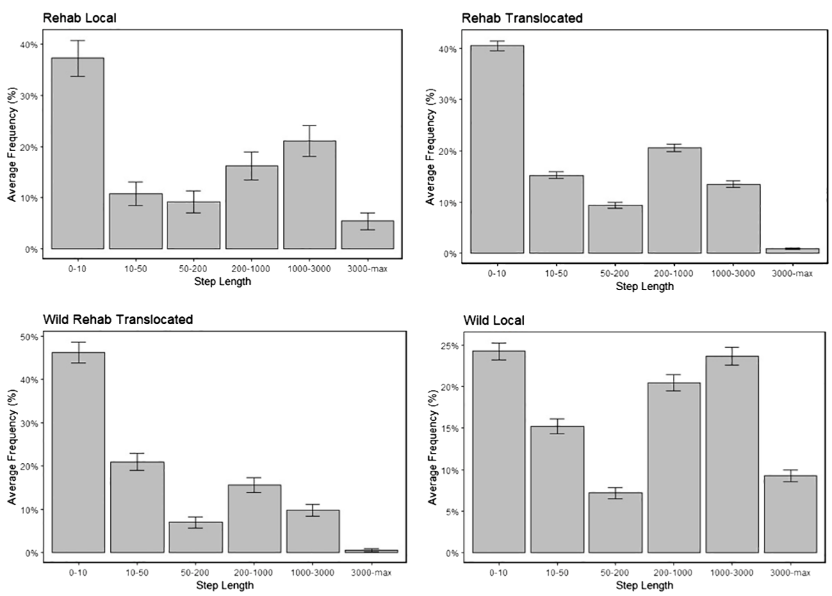

FIGURE 2
Histograms for step lengths of the four classes of cheetah. Average frequencies of step length represented as percentages, with error bars included for each class.

longer distances during the day and shorter distances during the night compared to crepuscular periods. Cheetahs moved shorter distances when far from waterholes.

3.2.3 Rehabilitated translocated

Only the Global Model (no marking tree) was supported for Rehabilitated Translocated individuals (Table 4; Supplementary Table S9). Results for steps intersecting habitat edge, day and night showed the same trend as Wild Local cheetahs. In addition, distance to edge and quadratic distance to edge were associated with step length, indicating that step length varied non-linearly with edge habitat.

3.2.4 Wild rehabilitated translocated

Only the Global Model 2 (Resource Movement) was supported (Table 4; Supplementary Table S10). These cheetahs moved longer distances during the day compared to crepuscular periods. Additionally, the cheetahs moved shorter distances when far from marking trees. Steps intersecting habitat edges were longer compared to those confined by the Big Field boundaries.

TABLE 4 Covariates associated with cheetah movements based on supported models ranked in an AICc framework (ΔAICc <2).

		Cheetah class							
		Wild Local (n=2)		Rehabilitated Local (n=2)		Rehabilitated Translocated (n=5)		Wild Rehabilitated Translocated (n=1)	
Hypothesis	Covariate	Estimate (SE)	*p*-value	Estimate (SE)	*p*-value	Estimate (SE)	*p*-value	Estimate (SE)	*p*-value
1	Intersection	0.74 (+/- 0.08)	<0.001*	0.60 (+/- 0.45)	0.18	1.07 (+/- 0.08)	<0.001*		
	Outside	-0.09 (+/- 0.07)	0.19	-0.21 (+/- 0.37)	0.57	-0.10 (+/- 0.05)	0.052		
	Waterhole	-0.03 (+/- 0.02)	0.29	-0.15 (+/- 0.07)	0.043*	-4.9e-3 (+/- 0.02)	0.80		
	Edge	-0.06 (+/- 0.08)	0.47	-0.16 (+/- 0.29)	0.57	0.25 (+/- 0.08)	<0.001*		
	Edge^2	0.13 (+/- 0.08)	0.09	0.19 (+/- 0.28)	0.52	-0.25 (+/- 0.07)	<0.001*		
	Day	-0.65 (+/- 0.05)	<0.001*	0.32 (+/- 0.16)	0.049*	-0.14 (+/- 0.04)	0.001*		
	Night	-0.28 (+/- 0.06)	<0.001*	-0.59 (+/- 0.18)	0.001*	-0.30 (+/- 0.05)	<0.001*		
3	Waterhole	-0.04 (+/- 0.02)	0.08						
	Day	-0.89 (+/- 0.05)	<0.001*						
	Night	-0.40 (+/- 0.06)	<0.001*						
6	Intersection	0.74 (+/- 0.08)	<0.001*						
	Outside	-0.06 (+/- 0.07)	0.42						
	Day	-0.66 (+/- 0.05)	<0.001*						
	Night	-0.27 (+/- 0.06)	<0.001*						
8	Waterhole	-3.2e-3 (+/- 0.02)	0.89					-0.08 (+/- 0.04)	0.077
	Marking tree	3.2e-3 (+/- 0.03)	0.88					-0.12 (+/- 0.05)	0.014*
	Intersection	0.74 (+/- 0.08)	<0.001*					1.74 (+/- 0.36)	<0.001*
	Outside	-0.06 (+/- 0.07)	0.43					-0.05 (+/- 0.24)	0.83
	Day	-0.66 (+/- 0.05)	<0.001*					0.52 (+/- 0.11)	<0.001*
	Night	-0.27 (+/- 0.06)	<0.001*					-0.20 (+/- 0.11)	0.080

Estimates for which confidence intervals did not overlap zero are highlighted with an asterisk.

3.3 Cheetah-prey relationship

Small prey did not vary significantly over time, whereas large prey did (W=36, p=0.029*) (Figure 3). In years of higher prey availability, including both grazer and browser ungulate species, cheetahs moved shorter distances (2013-2016) (Figure 4).

4 Discussion

The releases of cheetahs in our study system were carried out to augment a local population that persisted at low densities thought to be below carrying capacity, while simultaneously mitigating human-wildlife conflict at the sites where the released animals originated from. The releases of translocated individuals took place within existing cheetah range on CCF property which functioned as wildlife reserve, and contributed to the enhancement of the local population and presumably to ecosystem services therein (Fabiano et al., 2020). Some of the cheetahs released had initially been brought to CCF as orphaned cubs when their mothers were killed as part of human-wildlife conflicts, therefore post-release monitoring provided an ideal opportunity to compare the movement ecology of rehabilitated individuals to wild ones. We justify our categorisation of cheetahs through ecological rationale and variables included in our methodology, but acknowledge that large carnivores exhibit individual behavioural variability (Cristescu and Boyce, 2013; Shaw, 2020). Our sample size was insufficient to build individual models and to directly assess individual differences as well as influence of age within a given reproductive class. However, we did account for individual and reproductive class variability using a mixed-effects modelling approach (Supplementary Tables S14 – S16).

4.1 Movement metrics

Wild Local cheetahs exhibited significantly longer steps than other classes, which is contrary to our expectation that they would have shortest movements because of familiarity with the area and absence of exploratory movements. The extensive movement rates of Wild Local individuals might be attributed to enhanced territorial behaviour with the release of conspecifics in the same system. Cheetah releases occurred throughout the study duration, including releases when the wild local cheetahs were monitored (2007-2009). However, some of the releases involved VHF radiocollars and therefore could not be included in this study due to lack of GPS data for movement analysis. The large movement rates of Wild Local individuals could also reflect a hunting strategy that focuses on large prey which are present at low density and require extensive searches for movements.

Also contrary to expectations, released cheetahs that were unfamiliar with the area having been translocated displayed shorter movements, which might be suggestive of cautious exploratory behaviour. The difference in movement rates among cheetah classes suggest possible behavioural changes that may be triggered by environmental factors but also possibly by conspecific interactions, pointing to the need to understand the effects of releases on resident and introduced individuals in rewilding and reintroduction efforts. Differences in movement rates were recorded among sexes also, with male cheetahs having significantly longer step lengths than females, despite females maintaining larger home ranges in this species (Marker et al., 2007). Extensive movements by males may be a strategy for territorial defence (Weise et al., 2015).

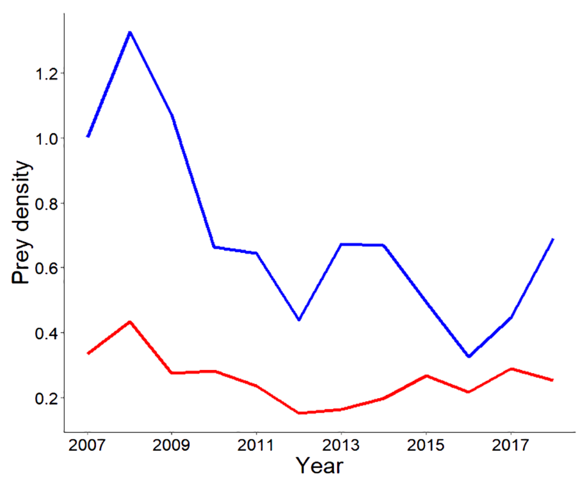

FIGURE 3
Prey density (per km^2) for small and large ungulate prey, calculated over time. The blue line represents large prey, and the red line represents small prey. Giraffe was excluded due to low likelihood of cheetah hunting this species, and Leporids, ostrich and secretary birds excluded due to few observations precluding calculation of the estimated strip width from distance sampling. .

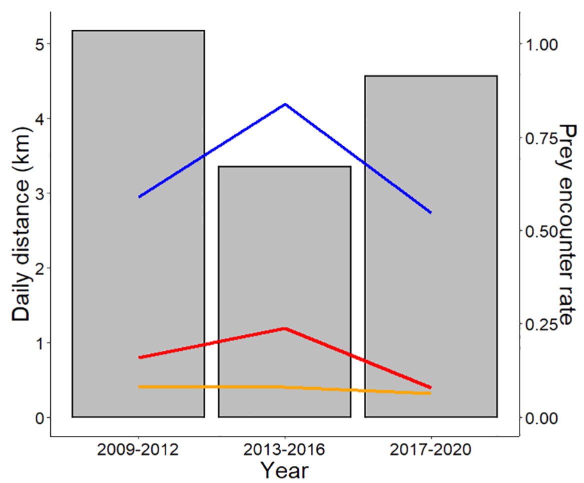

FIGURE 4
Daily distance (km) moved by cheetahs in four-year increments: 2009-2012 (n=2), 2013-2016 (n=5), 2017-2020 (n=2). The prey encounter rate (prey per km^2) is displayed on the secondary y-axis, with results represented by lines split into three prey categories. Ungulate prey according to foraging strategy included mixed feeders (n=2), grazers (n=5), and browsers (n=3). The blue line represents grazers, the red line represents browsers and the orange line represents mixed feeders.

4.2 Factors associated with movements

Although classically considered to be diurnal hunters, with bouts of crepuscular activity (Hayward and Slotow, 2009; Nghikembua et al., 2016), cheetahs have been demonstrated to be flexible in activity patterns and can have nocturnal movements where dominant large carnivores are absent or where they are heavily persecuted by humans. Cheetahs can be particularly active during lunar cycles with increased moonlight, a strategy thought to increase nocturnal hunting efficiency (Broekhuis et al., 2014; Searle et al., 2021). Our findings on cheetah movements show a predominance of long movements during the crepuscular period, which might place them at risk of encountering a dominant competitor, the leopard (Verschueren et al., 2021).

Rehabilitated Local individuals were the only ones for which movements were associated with waterhole proximity, but in the opposite pattern than we had anticipated. When close to waterholes, this class of cheetahs moved greater distances than when far from waterholes, possibly indicating that proximity to waterhole may not be desirable. Although waterholes are key resources for many large carnivores (Jhala et al., 2021) for hydration and hunting opportunities, they may especially be sought after by ambush predators (Crosmary et al., 2012). The cheetahs in this category were solitary and familiar to the area, thereby presumably aware that waterholes increase the likelihood of encountering leopards (Krag et al., 2023). Leopards are the dominant predator and are highly abundant in this system (Cheetah Conservation Fund, unpublished data). Wild local cheetah individuals may not have shown the same pattern due to being part of male coalitions, which are at lower risk from leopards due to group living. Nonetheless, ungulates in our study system appear to adjust their waterhole visitation patterns with cheetah presence (Ruble et al., 2022), suggesting a potential response to perceived predation risk. For rehabilitated local individuals, the movements here may be determined by prey distribution as certain species of prey are more water-dependent than others (Kihwele et al., 2020), but for this study we lacked the information to confirm spatial prey availability by cheetahs.

Distance to confirmed marking trees was associated with step length of the one Wild Rehabilitated Translocated cheetah included in the study, which moved longer distances when close to the marking tree. As a translocated cheetah, this female was unfamiliar with the area and minimising the time spent around marking trees might have been part of a strategy of risky conspecific avoidance involving resident male(s). Cheetahs, particularly males use marking trees repeatedly for territorial and reproductive advertising (Marker-Kraus and Kraus, 1997), whereas in leopards both sexes often scent mark (Cornhill and Kerley, 2020). Cheetahs and leopards often choose the same marking trees but exhibit temporal segregation to avoid conflict (Rafiq et al., 2020; Verschueren et al., 2021).

The movements of Rehabilitated Translocated cheetahs in relation to the hard edge between human-managed open savanna and bush encroached woodland savanna revealed a non-linear relationship. Habitat edges are often favoured by prey and also provide concealment, which can assist in hunting (Bissett and Bernard, 2007; Atkinson et al., 2022b).

4.3 Cheetah-prey relationship

Our study system experienced a decline in large prey over time and we were able to detect an adjustment in movement rates by cheetahs particularly in relation to the variability in browser and grazer ungulates. As resource availability fluctuates, cheetahs must adapt their ecological and behavioural processes (Broekhuis et al., 2019, Broekhuis et al., 2021; Rodriguez-Recio et al., 2022). Our data support the resource dispersion hypothesis, which predicts that large carnivores will expand their ranging patterns as resource availability becomes dispersed, resulting in increased movements (Macdonald, 1983; Farhadinia et al., 2016; Rodriguez-Recio et al., 2022).

4.4 Recommendations and conservation applications

Post-release monitoring of the behaviour of apex predators released as part of rewilding or reintroductions remains challenging and has rarely been compared with behaviours of locally resident animals. Based on a dataset of released and resident GPS radiocollared cheetahs and prey populations monitored over >10 years, we were able to draw inferences on factors that affect apex predator movements and began to explore the complexity of predator-prey relationships. We found extensive differences among cheetahs regarding their movement rates in relation to their familiarity with the area, rehabilitation, and ecological factors. We recommend that rewilding and reintroduction programmes monitor individuals closely using GPS tracking technology to understand movements and, for population augmentation projects, the potential effects on the resident population.

High movement rates in males suggest that it would be beneficial to rewild female cheetahs initially as they have shorter movements, and those females may encourage residency in future releases of males. Less expansive movements can be beneficial for cheetah survival in unprotected areas (Sievert et al., 2022; Cristescu et al., submitted). For example, roads pose a dynamic threat to individuals that cover extensive distances, and road density and type become paramount during the selection of individuals for release. This is due to the fact that roads contribute significantly to the mortality of wild individuals (Mohammadi et al, 2018; Mohammadi and Kaboli, 2016). Cheetahs that move longer distances, particularly through extensive exploratory behaviour, are most vulnerable to encountering risky situations through human-wildlife conflict. Our study highlighted that males in coalitions undertake longest movements, and territorial males will repeatedly use specific areas to advertise their presence and mark their territory in communication hubs (Caro, 1994; Melzheimer et al., 2020). We recommend farmers remove their livestock from these known areas, and that livestock should not be free-ranging during crepuscular or night-time periods, to avoid the most frequent activity periods of large carnivores such as cheetahs, leopards, and hyenas (Puls et al., 2021; Vissia et al., 2021, Vissia et al., 2022). Removing livestock late afternoon and releasing them again in the morning would be a good strategy for conflict mitigation. Because the success of release projects for apex predators relies heavily on prey abundance and accessibility, research could benefit from incorporating observations of diet composition and prey preference, as well as kill frequencies and kill intervals by predator age and sex class (Cristescu et al., 2022).

Although focal studies such as ours are informative behaviourally by incorporating detailed parameters such as location of marking sites and waterholes and detailed knowledge of habitats, conducting movement analyses on a broader landscape scale has its own set of advantages. A great opportunity is the availability of remote sensing data, which can be used to relate animal movement trajectories to landscape characteristics over extensive regions.

Rewilding landscapes through the restoration of species that either went locally extinct or experienced significant declines is an increasingly applied practice in biological conservation. We encourage researchers to continue to investigate the post-release movement ecology of apex predators and the effects of released animals on the food webs and ecosystems at the release sites, while not neglecting resident individuals that might be present at the sites.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by National Commission on Research, Science and Technology, Government of Namibia. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

JD: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft. BC: Conceptualization, Methodology, Resources, Supervision, Writing – review & editing. KB: Formal analysis, Methodology, Writing – review & editing. NR: Conceptualization, Supervision, Writing – review & editing. LM: Resources, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1351366/full#supplementary-material

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Developing guidelines and a theory of change framework to inform rewilding application

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Introduction: There remain a number of debates and conflicts about the concept of rewilding which can be barriers to its application. Some of these conflicts stem from the variety of contextual interpretations of rewilding, leading to conflict between rewilding theories and approaches. Conclusions have also been drawn about rewilding based on limited case studies, so that emergent rewilding theories aren't applicable to all rewilding projects, limiting their support in the field. Past theories have distinguished different types of rewilding, encouraging debate over the proposed methods, although in practice these approaches often share similar goals and use similar interventions. One barrier to achieving consensus in the practice of rewilding is that there are no clear guidelines for rewilding, and there are limited broad-scale studies focusing on how rewilding is practiced. This paper addresses this by offering the first broad study of rewilding guidelines and interventions.

Methods: A grounded theory study was undertaken, using data sourced from rewilding organisations, case studies, and research. Expressions were coded in the data relating to intentions for how rewilding should be practiced and the interventions used.

Results: Drawing from these data, the paper offers three tools to guide rewilding practitioners: (1) an overview of guidelines for rewilding practice, (2) a list of interventions used in rewilding, considering them against rewilding goals, (3) a theory of change framework to guide rewilding application.

Discussion: The tools presented here will inform work towards IUCN rewilding guidelines. Several areas that require further consideration are highlighted. We hope that this initial study of application can improve agreement and collaboration among the rewilding community.

KEYWORDS

rewilding, adaptive co-management, theory of change (ToC), transformative conservation, ecological restoration

1 Introduction

It has been suggested that a lack of clarity regarding the concept of rewilding (e.g. definitions, key principles) remains a barrier to rewilding application (Cózar-Escalante, 2019; Dandy and Wynne-Jones, 2019; Jones and Comfort, 2020). Some progress is being made towards consensus, as demonstrated by the IUCN CEM guiding principles and definition, which highlight social and ecological goals and implications for rewilding practice (Carver et al., 2021). However, there remain several existing and emerging debates or perceived paradoxes that demand our attention. Some of this confusion and/or conflict is caused by conceptual "stretching"; whereby rewilding is being altered to align with the values, perceptions, or priorities of those promoting rewilding, perhaps to appeal to stakeholders, or align with existing policy (Deary and Warren, 2019; Holmes et al., 2020; Wynne-Jones et al., 2020; Martin et al., 2021; Thomas, 2022). For example, in an empirical study of two rewilding projects in England, Thomas (2022) demonstrates that rewilding is being "domesticated", with its more radical potential being moderated for the English context. Whilst stretching is not necessarily problematic, as there is a stated need for rewilding to be adaptable to different contexts (Carver et al., 2021), the issue here is that rewilding is continually judged by how it is practiced in the present and what is pragmatically possible within the current paradigm and culture, thus limiting the resulting definitions and conceptualisations. For example, Dempsey (2021) undertook a study of rewilding at Knepp Wildland to measure existing levels of human control over natural processes. They conclude that based on the Knepp example, rewilding does not necessarily represent reduced human control of nature, due to management of ecological trajectories at Knepp to achieve a desired outcome of wood pasture in an English landscape. While the interrogation of notions of control is warranted and welcome, current levels of control in one project are not a fair representation of rewilding aspirations, limiting the validity of the conclusion drawn. This trend has led to a perceived paradox being reflected in the literature between rewilding's transformative[1] goals and a need for pragmatism in its application, with concerns that desired paradigm shifts are being compromised in rewilding practice and policies, alongside concerns that rewilding interventions may lead to unwanted social or ecological outcomes (Delibes-Mateos et al., 2019; Genes et al., 2019; Holmes et al., 2020; Wynne-Jones et al., 2020). This demonstrates a need to expand conceptualisations of rewilding, to consider its aims and motivations alongside its practice. This may help to specify and address perceived conflicts between aims, current practices, and underpinning ethics.

To address the issues highlighted above, we conducted a broad-scale study of rewilding to identify common themes emerging from various data sources related to rewilding practice and theory. While we consider the results relating to rewilding's transformative goals elsewhere (Hawkins, 2022; Hawkins, 2023; Hawkins et al., in prep.[2]), this paper presents a study of rewilding application. Data includes a survey of rewilding leaders (those leading rewilding projects, organisations, and research) and influential texts that have guided rewilding application in different geographic locations, which include references to and case studies of many rewilding projects. Drawing from these data, the paper offers three tools to guide rewilding practitioners: (1) an overview of guidelines for rewilding practice, (2) a list of interventions used in rewilding, considering them against rewilding goals, (3) a theory of change (ToC) framework to guide rewilding application. This framework addresses the perceived paradox highlighted above, demonstrating that rewilding is a balance between transformative goals and place-based pragmatism. These tools act as a basis to inform the work towards IUCN rewilding guidelines. One barrier to achieving consensus in the practice of rewilding is that there are no clear guidelines for rewilding, and there are limited broad-scale studies focusing on how rewilding is practiced. Past studies have chosen to separate different approaches to rewilding, i.e., 3Cs rewilding (cores, carnivores, corridors), trophic rewilding, passive rewilding, ecological rewilding (e.g., Pettorelli et al., 2018), however, we feel these distinctions are unhelpful and can cause unnecessary conflict, as many rewilding projects have similar goals and use similar interventions despite these distinctions. The hope is that the tools presented here can affect some agreement and collaboration among the rewilding community.

2 Method

Grounded theory (GT) is a form of exploratory research (Glaser and Strauss, 1965; Stebbins, 2001), guided by the precept that to understand any phenomenon well it is necessary to start by looking at it in broad, nonspecialized terms and to search for understanding wherever it may be found. In practice GT is an inductive/abductive approach which allows for flexible data collection and analysis, with the researcher exploring data for patterns, ideas, or hypotheses (Stebbins, 2001; Creswell, 2007; Charmaz, 2014). The intention is to produce inductively derived generalizations about the topic under study, and to weave these generalizations into a "grounded theory" that goes some way to explaining the phenomenon as experienced by people operating within (Stebbins, 2001; Creswell, 2007; Charmaz, 2014).

2.1 Data collection

GT allows for flexibility when it comes to sources of data, which can include interviews, surveys, and existing texts or secondary material (Bryant and Charmaz, 2019). Given that there were

1 Transformative change is described as a "fundamental, system-wide reorganization across technological, economic, and social factors, including paradigms, goals, and values and is promoted as essential to achieving global sustainability" (IPBES, 2019).

2 Hawkins, S., Convery, I., and Carver, S. (in prep.) A study of rewilding aims: Integrating coexistence into a rewilding continuum.

limitations to data collection brought about by COVID while data collection was ongoing, we decided to focus on a desk-based study, drawing on two accessible data sources: existing results from a rewilding pioneer survey (RPS) and influential rewilding texts (IRT).

2.1.1 Rewilding pioneer survey

The RPS serves as the initial data collection method and was originally designed to support the work of the IUCN Commission for Ecosystem Management Rewilding Thematic Group (RTG) in developing guiding principles for rewilding (Carver et al., 2021). The existing RPS data presented an opportunity for further investigation, as its previous analysis had been constrained by its focus on guiding principles.

The survey targeted individuals recognized as influential figures in the development of the rewilding field, referred to as "rewilding pioneers." These pioneers were identified based on their contributions to rewilding projects, literature, or research, and through a snowball sampling method. Specifically, they were identified through authorship of rewilding publications, self-identification through contact with the RTG, and a survey question asking for participant recommendations. The survey encompassed 19 predominantly open-ended questions and included six questions related to demographic information and contact details. It was conducted in 2018, yielding 60 responses (out of 126 invitations to participate). Participants represented diverse backgrounds, including academics, authors, and practitioners from various disciplines, with many associated with well-known rewilding organizations or widely cited rewilding publications. The participant composition leaned towards North American and Western European individuals, aligning with the survey's focus on "pioneers" and the historical roots of rewilding in the USA and Western Europe since the 1980s. Ethical approval was obtained from the University of Cumbria research ethics panel prior to participant recruitment (Hawkins, 2023).

2.1.2 Secondary material: influential rewilding texts

The second data set consists of texts cited by RPS respondents. These texts are referenced in response to various RPS questions, with many responses prompting further exploration of these influential texts. The IRT encompasses 10 journal articles, nine non-peer-reviewed articles (including policy briefs, magazine articles, and speeches), six single-author books, four edited books, and an additional book chapter. A comprehensive list can be found in Supplementary Table S1.

Given the breadth of texts identified in the RPS, all texts cited in the RPS were used and this allowed us to delimit a clear set of influential texts among a proliferation of literature in rewilding and related fields. This also allowed us to include influential "grey" literature that is often overlooked in literature reviews. The texts provide valuable insights from influential figures on the rewilding concept, address gaps in cases where influential figures had not participated in the RPS, and represent a range of influential rewilding organizations or projects.

2.2 Data analysis

Given the nature of GT and the emphasis on exploring data through coding to inform emerging theories (Bryant and Charmaz, 2019), both sets of data were treated as qualitative data and the results presented combine findings from the RPS and IRT data. The data analysis process was conducted using Nvivo 12 to categorize the data under three parent nodes focusing on the concept of change: "change what" (aims and intentions of rewilding), "change why" (context and drivers), and "change how" (rewilding interventions and practical guidance). These three nodes align with the basic categories in a ToC (see section 2.3). This article primarily presents the findings related to the parent node "change how" which comprised two sub-categories – interventions and guidelines. The proposed ToC framework emerged as a theory drawing from these sub-categories.

RPS data coding was carried out during 2020, resulting in the creation of an initial ToC (Hawkins, 2022). Subsequently, IRT data collection and coding took place over 2021 and 2022. This second dataset allowed for a deeper exploration through focused coding (Charmaz, 2014), leading to further refinement, analysis, and conceptualization of the initial codes. Focused coding involves examining how initial codes account for the data, enabling the synthesis, analysis, and conceptualization of larger data segments (Charmaz, 2014). During this process, codes became more precisely defined, sub-nodes emerged, and certain categories were repositioned under different parent nodes, while the overarching parent nodes remained consistent.

Throughout all stages of coding, the researcher employed memoing as recommended by Charmaz (2014). Memoing involved spontaneous, unedited writing to capture reflections, emotional responses, emerging theories, connections between nodes, and encountered challenges. It played a vital role in keeping the researcher engaged with the data analysis, overcoming obstacles, identifying emerging theories and connections, and maintaining momentum.

2.3 Theory of change

ToC is an outcomes-based framework which was initially developed to aid agencies concerned with creating long-term social change, encouraging them to create a vision for the future which can be used to plan interventions and demonstrate causal links and sequences of events needed to lead to that desired outcome. In short it "provides a roadmap to get from here to there" (Centre for Theory of Change), mapping the steps that must be taken between the present context and the desired future (Biggs et al., 2017; Centre for Theory of Change). ToC is increasingly used across different sectors and disciplines, including conservation, environmental decision making, and conflict management (Allen et al., 2017; Baynham-Herd et al., 2018). The models or instructions for creating ToCs vary, but the main components are similar (Figure 1).

It has been suggested that a route to unifying global rewilding and promoting its transformative potential is to focus on shared

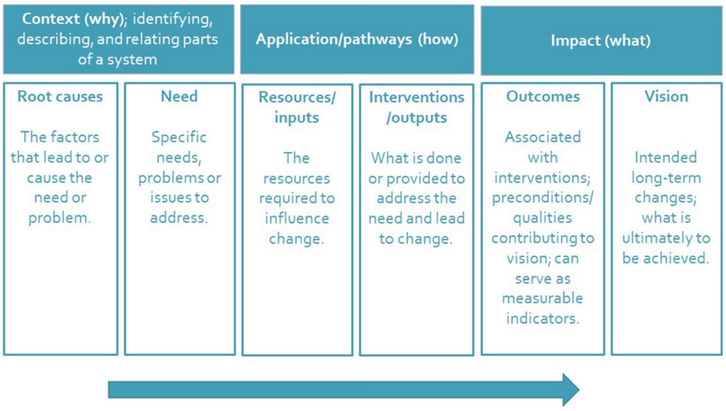

FIGURE 1
Suggested components of a ToC (adapted from Biggs et al., 2017; Ghate, 2018; Reinholz and Andrews, 2020).

goals (Pettorelli et al., 2019; Carver et al., 2021; Hawkins et al., 2022). These goals can provide a vision on which to focus the development of a rewilding ToC. The nature of the themes emerging from the data and the emphasis on theory creation in a CGT approach further justify the adoption of a ToC framework to represent the grounded theories emerging from this research.

3 Results

3.1 Guidelines for rewilding practice

Many drivers of rewilding relate to a desire to change the culture and practice of conservation biology and related institutions (Carver et al., 2021; Hawkins, 2022). These include concerns that some practices promote human-nature dualism (Ward, 2019), objectives based on pre-determined conditions (Taylor, 2011), anthropocentrism (Noss, 1992), and ineffective practices that do not acknowledge complex ecological interactions (Soule and Noss, 1998). Given that the data were sourced from influential rewilding practitioners or organisations, several themes emerging from the data analysis expressed strong views for how rewilding *should* be practiced, reflecting the intentions for paradigm shifts in the conservation and restoration of nature. These have been thematically analysed and the themes are presented below as guidelines to inform rewilding application.

However, throughout this section it is noted that the intentions are difficult to achieve in practice. Therefore, this list of guidelines acts as a baseline study to inform future research on how to overcome barriers to achieving genuine change in how rewilding is applied.

3.1.1 Be transformative and visionary

The ambitions for rewilding are considered by some to be outside of what is accepted or comfortable within a current system or culture (e.g., Soule and Noss, 1998; Foreman, 2004; Monbiot, 2013), echoing intentions or potential for rewilding to promote paradigm shifts in policy, culture, or nature conservation (Soule and Terborgh, 1999b; Taylor, 2011; Pettorelli et al., 2018; Hawkins et al., 2022; Taylor et al., 2022). For example, the goals of rewilding organisation Trees for Life are described as stretch goals, "which may seem overly ambitious viewed from the current paradigm, but can be achieved with bold, creative thinking, strategic planning, and a willingness to think outside the box" (Puplett, 2008). This is reflected in principle 10 of the RTG principles (Carver et al., 2021), which focuses on a paradigm shift in the coexistence of humans and nature, with related institutional paradigm shifts.

Many rewilding organisations create ambitious visions for the future (Foreman, 2004; Helmer et al., 2015) and Noss (1992) describes rewilding as a vision toward which to strive over decades. The data show that there is intent behind the use of bold visions, i.e., to promote hope, innovation, and inspiration. As an example, Soule and Terborgh (1999b) write, "An inspiring vision is essential. In the frenetic, noisy years ahead, only such visions will attract attention and kindle hope." Those leading rewilding projects are encouraged to create visions for rewilding, considering ecological restoration and overcoming largely social barriers to rewilding (Weber Hertel and Luther, 2023), thereby combining social, ecological, and systemic change (Hawkins, 2022).

3.1.2 Be pragmatic, work iteratively

The visionary and transformative goals of rewilding are reconciled with pragmatism through iterative progression, whereby appropriate interventions are applied successively to progress a system towards a bold vision. Intentions for rewilding to be pragmatic (e.g., Soule and Terborgh, 1999b; Jepson et al., 2018) and to progress iteratively along a scale of rewilding (e.g., Bakker and Svenning, 2018; Butler et al., 2021) are expressed in the data. This reflects conceptualisations of rewilding as a continuum or scale, with the intention to move systems along a scale towards rewilding goals (Holmes et al., 2020; Carver et al., 2021). Jepson and Schepers (2016), for example, suggest that rewilding is:

> "a graduated and situated approach, where the goal is to move up a scale of wildness within the constraints of what is possible,

> and interacting with local cultural identities … Rewilding is not a state; it is a process. It is about moving up a scale of wildness and giving the ecosystems a functional 'up-grade' whatever their nature, scale, and location."

Future rewilding guidelines may wish to draw on agile project management (Fernandez and Fernandez, 2008) and adaptive governance frameworks (Butler et al., 2021) which are both intrinsically iterative to provide guidance for how to integrate iterative progression into rewilding practice.

3.1.3 Be place-based

Every social-ecological system (SES) or landscape will offer a unique context, with their own opportunities for or barriers to rewilding. Hence, place-based approaches and thorough assessments of local social-ecological conditions are key to developing rewilding plans and prioritizing interventions (Ceausu et al., 2015; Navarro and Pereira, 2015b; Butler et al., 2019). This is reflected in contextual assessments (e.g., Soule and Terborgh, 1999a; Foreman, 2004; Cerqueira et al., 2015; Jepson et al., 2018) and considerations for ecological or cultural conditions that influence what interventions are appropriate, e.g., a natural seed source influences the potential for natural regeneration (Navarro et al., 2015), or culturally significant species enhance opportunities for species reintroductions (Monbiot, 2013; Jepson et al., 2018; Heuer et al., 2023). Thorough and genuine place-based assessments of socio-cultural factors allow projects to avoid making assumptions about levels of support, stakeholder priorities, or reasons for opposition. This guideline encourages practitioners to develop rewilding plans after contextual assessments are made, rather than approaching areas with pre-conceived notions of what interventions should be used. Even when a certain intervention may be desirable, it is not prioritised or applied ahead of interventions that are more suited to the current context. This may also help to address negative perceptions of rewilding as practitioners are encouraged to address existing socio-cultural barriers to rewilding prior to or in tandem with other interventions (Weber Hertel and Luther, 2023).

3.1.4 Think large-scale and long-term

Emerging ecological theories considering the requirements of large, wide-ranging mammals, prompted large- or landscape-scale implications for rewilding (Soule and Terborgh, 1999a; Carver et al., 2021). This reflects a move from traditional conservation which tended to focus on delimited areas based on habitat type (Soule and Noss, 1998; Taylor, 2011). Soule and Terborgh (1999b), for example, encourage rewilding practitioners "to think and plan on scales that transcend traditional political boundaries … and familiar spans of time."

Thinking large scale requires practitioners to acknowledge the multiple requirements of diverse (human and non-human) inhabitants of a landscape, considering social factors alongside ecological ones. Hence this guideline encourages a more systemic and interdisciplinary practice (linked to systems thinking in section 3.1.5).

Long-term perspectives require consideration for the longevity of projects, for example going beyond limitations associated with short-term funding or goals (Johns, 2019). To enhance sustainability, it is suggested that projects are integrated into the fabric of the system (Saunders, 2011; Jepson et al., 2018). This includes considering how funding and resourcing for rewilding can be integrated within a system (Groom et al., 1999; Donlan et al., 2005; Gow, 2006; Jobse et al., 2015), so that finite and external funding is less critical. However, examples demonstrate that longevity is not just about economic sustainability but also about engendering a sustainable culture suited to the place, seeking to reform existing industry or resource use, for example hunting, forestry, or mining (Jepson et al., 2018). For example, Parfitt (2006) highlights the WWF Netherlands Living Rivers project which introduced clay extraction as a new economic driver which could (partly) substitute the declining role of agriculture, contribute to the ecological restoration of the riparian landscape, and contribute to improved and sustainable flood prevention. McKibben (1995) demonstrates the potential for reform in commercial forestry to mitigate rising unemployment and rural poverty while improving ecological conditions in traditional logging areas.

3.1.5 Use systems thinking

Working at a large scale accentuates the complexity associated with nested systems, so that rewilding surpasses geographic, ecological, or disciplinary boundaries, acknowledging the complexity and diversity reflected in the concept of SES (Biggs et al., 2021). Reflecting a trend towards holism and SES framings of rewilding, systems thinking is increasingly encouraged in rewilding theory (Butler et al., 2021; Jones and Jones, 2023). The emphasis on scale drove the integration of socio-cultural elements of landscapes into rewilding. This is reflected in guidance on how to address socio-cultural factors in rewilding across the data and wider literature (Groom et al., 1999; Foreman, 2004; Jepson et al., 2018; Linnell and Jackson, 2019; Weber Hertel and Luther, 2023) and reflections on complex interactions between ecological and socio-political factors effecting the potential for rewilding at larger scales (Soule and Terborgh, 1999b; Taylor, 2011; Pettorelli et al., 2018; Johns, 2019). In this way, landscapes can be considered as SES. Systems thinking also creates the potential for rewilding to be applied to systems that are not associated with a spatial area. For example, in relation to the culture of education (Prince, 2022) or recreation and adventure travel (Loynes, 2022), perhaps offering the potential to "rewild" the culture and practice of rewilding.

While this guideline overlaps with a number of the other guidelines presented here, we felt it important to highlight separately as the integration of complexity in practice is hindered by a wider lack of knowledge, methods, or skills for systems thinking. It requires moving from a current paradigm which tends to simplify, towards a paradigm that considers complexity. This is identified as a priority for research to inform rewilding, restoration, and sustainability science (Biggs et al., 2017; Butler et al., 2021; Jones and Jones, 2023; San Miguel, 2023). Iterative, agile project management and ToC frameworks seek to address these issues in many different disciplines (Fernandez and Fernandez, 2008; Allen et al., 2017) and may help rewilding projects to integrate complex systems thinking, long-term transformative change, transdisciplinarity, and collaboration. There is also evidence to suggest that holistic, systems thinking is inherent in some indigenous knowledge systems and philosophies (Cusicanqui, 2012; Berkes, 2017; Fenton and Playdon, 2022), highlighting an imperative to address institutional biases in pursuit of inclusive, globally applicable rewilding policy and guidance.

3.1.6 Be adaptive, embrace uncertainty and indeterminacy

This guideline reflects a desire to address values for control, order, and predictability that is highlighted as a concern in the data (e.g., Taylor, 2011; Monbiot, 2013). In response, rewilding asks practitioners to accommodate uncertainty, indeterminacy, and change.

An important implication for rewilding application is that rewilding has no end point or predetermined compositional objectives. This is best described by Monbiot (2013, p. 168):

> "Rewilding has no end points, no view about what a 'right' ecosystem or a 'right' assemblage of species looks like. It does not strive to produce a heath, a meadow, a rainforest, a kelp garden, or a coral reef. It lets nature decide. The ecosystems that will emerge, in our changed climates, on our depleted soils, will not be the same as those which prevailed in the past. The way they evolve cannot be predicted, which is one of the reasons why this project enthrals."

This reflects complex systems thinking that encourages no end point and is associated with the need to accommodate greater levels of uncertainty and indeterminacy (Fougères et al., 2022; Jones and Jones, 2023), and emerging ecological theories that emphasise change [e.g., alternative stable states (Beisner et al., 2003) and novel ecosystems (Klop-Toker et al., 2020)]. This has caused some debate in rewilding literature over the concepts of reference ecosystems and novel ecosystems (e.g., Pettorelli et al., 2018; Genes et al., 2019). The results presented here address this conflict by demonstrating that reference ecosystems are not intended to serve as ecological aims for rewilding projects, but rather provide historical evidence of coevolution to inform rewilding interventions (see section 3.1.7). This is important as this conflict remains prevalent in the data, which show that while rewilding application seeks to embrace uncertainty and indeterminacy in theory, pragmatism and personal preference are barriers to achieving this in practice as some rewilding projects remain prescriptive about habitat types, e.g., projects that seek to create wood pasture (Vera, 2000; Kirby et al., 2004; Dempsey, 2021). Related projects such as Knepp and Oostvardersplassen have been criticised for being led by human priorities and for limiting the potential for natural autonomy (Kopnina et al., 2022; Leadbeater et al., 2022), but are also promoted for their positive impacts on ecological function, biodiversity, and natural autonomy, according to the RPS data. It is suggested that tolerance for adaptability and uncertainty and allowing nature to lead restoration (see section 3.1.9) are key leverage points for achieving a more adaptable, non-determinist rewilding practice. More targeted, longitudinal studies are required to understand whether human preferences and habitat-focused objectives are a barrier to achieving rewilding aims and to identify social or ecological barriers that limit indeterminacy in rewilding application.

Another concern acknowledged in the data coded to this node is that there remains uncertainty over how best to approach rewilding. This guideline therefore encourages trial and error as new methods are developed or new knowledge or realisations are made, rather than a desire to know and predict the outcome of an intervention before it is applied (Noss, 1992). Knowledge, best practice, and definitions of concepts evolve, as is demonstrated by the concept of rewilding (Gammon, 2018). Embracing indeterminacy may offer a route to reduce conflict related to different interpretations of or approaches to rewilding and instead encourage creativity, collaboration, and knowledge sharing despite divergences. This highlights the need for rewilding guidelines to also be adaptable. The guidelines and framework suggested here offer routes to unifying practice without being prescriptive of ecosystem composition.

3.1.7 Collect evidence and monitor rewilding to inform adaptive plans

While the above guideline asks practitioners to be adaptable and embrace uncertainty, this guideline encourages the use of evidence to inform practice in the absence of proof or certainty. Early conceptualisations of rewilding called for rewilding practice to be science based (e.g., Noss, 1992; Vera, 2000). This emphasis continues to be reflected throughout the data, however, there are increasingly calls to integrate other forms of evidence, as reflected in principle 7 of the existing guiding principles (Carver et al., 2021) which states that rewilding is informed by science, traditional ecological knowledge, and other local knowledge. This forms part of a movement towards knowledge democracy and transdisciplinarity in conservation and environmental management (Berkes, 2009; Fenton and Playdon, 2022; Raymond et al., 2022). However, it is suggested here that the term "evidence" is used as a democratic word, avoiding issues associated with terms that seek to legitimate and distinguish between knowledge types, such as the term "traditional ecological knowledge" (Fenton and Playdon, 2022).

Different types of evidence, reflecting different scales or emphases, are required to inform rewilding application. At a policy level, evidence is provided from research, academic literature, frameworks, and related policies. At a local scale, and reflecting that rewilding is place-based (section 3.1.3), those driving rewilding must seek local evidence to inform the choice and prioritisation of rewilding interventions. Initial assessments provide a baseline for the project, while ongoing monitoring assesses the impacts of rewilding interventions and identifies emerging opportunities or barriers around which to adapt rewilding plans.

There are monitoring examples and suggestions for evidence in the data, including historical evidence, such as reference ecosystems

(Genes et al., 2019; Carver et al., 2021) or evidence of historical land use and change; baseline ecological surveys; social studies that consider stakeholder preferences or values; or social or ecological feasibility studies. Methods used to monitor rewilding projects vary and are influenced by project priorities and resource availability, from less intensive, traditional ecological survey methods such as those undertaken at Carrifran Wildwood (Adair and Ashmole, 2022) to intensive, innovative monitoring techniques including remote sensing, eDNA, and natural capital accounting approaches as undertaken at Birchfield (White et al., 2022). While evidence and monitoring are typically viewed as essential to inform practice and improve knowledge of rewilding (Groom et al., 1999; Svenning et al., 2016; Pettorelli et al., 2018; Corlett, 2019), establishing monitoring guidance for rewilding in complex systems remains a challenge (Root-Bernstein, 2022; White et al., 2022) that reflects a paradigm shift from command-and-control approaches towards the need to embrace uncertainty and indeterminacy as highlighted in section 3.1.6. For example, Corlett's (2019) consideration of monitoring reflects traditional forms of project management and monitoring, reliant on "SMART" objectives (specific, measurable, achievable, relevant, and time-bound), which conflicts with emergent conceptualisations of rewilding as long-term, adaptable, and indeterminate (Butler et al., 2021; Root-Bernstein, 2022).

This is an area that requires further work to inform monitoring guidelines, which should seek to include a variety of methods to suite varying project resources and consider the indeterminate nature of rewilding. Although these may be flexible, some level of standardisation would aid knowledge and data sharing to inform rewilding research and best practice. Work towards monitoring guidelines could draw on methods for monitoring complex systems (UNDP Strategic Innovation, 2022) or might consider establishing core common outcomes, a concept initially used in medical fields but increasingly used in restoration (e.g., Reed et al., 2022), to provide a standardized framework for monitoring and evaluation.

3.1.8 Be inclusive and collaborative

The intention for rewilding to be inclusive and collaborative is highlighted in the data in response to calls to counteract exclusivity, injustice, and inequity in conservation (e.g., Monbiot, 2013; Ward, 2019). Counter to command-and-control approaches (Holling and Meffe, 1996; Briggs, 2003), rewilding practitioners are encouraged to see themselves as part of a system, collaborating with others to achieve rewilding goals, rather than as external entities that are furnished with power to make decisions effecting the wellbeing of others (Martin et al., 2023). The data reflect that inclusive approaches could counteract perceptions that rewilding is exclusive and improve support for rewilding. But it is emphasised that rewilding practice looks beyond superficial notions of inclusivity that merely seek to promote rewilding to a community or demonstrate stakeholder support for rewilding to influence decision makers. Inclusion promotes transdisciplinarity, involvement of a diverse range of stakeholders, and deeper engagement with place (see section 3.1.3).

Increasingly, the perspectives and contributions of non-human species to rewilding are also being considered (Irwin, 2021; Bekoff, 2022; Kopnina et al., 2022; Moyano-Fernández, 2022), suggesting that holistic worldviews that view landscapes as collaborations among humans and other species can promote more sustainable practices (Washington et al., 2017). This has raised the importance of paradigm shifts in how humans relate to the rest of nature, "personal rewilding," or the "rewilding of hearts and minds" promoted in the data and elsewhere (Carver et al., 2021; Rawles, 2022) along with considerations for how this might be applied in practice (Maffey and Arts, 2022; Taylor et al., 2022). This is reflected in the interventions used within rewilding, which seek to promote ecological knowledge, human-nature connection, or coexistence (see section 3.2). This guideline therefore encourages practitioners to move from dualistic perceptions and a language of human dominance or control that can lead to objectives to remove all human influence, towards a language encouraging collaboration and coexistence to achieve system sustainability. Promoting place-based approaches may help with this and further longitudinal studies are required to understand how holistic worldviews, or transitions towards more holistic worldviews, influence system sustainability and resilience, while being mindful of risks of oversimplification, misinterpretation, and cultural and knowledge appropriation (Battiste and Henderson, 2000; Berkes, 2017; Schmitt et al., 2021; Fenton and Playdon, 2022).

In practice, opportunities for and extent of inclusivity or collaboration will vary depending on the scale and the context. Some rewilding projects may be small with no obvious human stakeholders other than those driving the project. However, this guideline encourages projects to look beyond the geographical limits of their projects or limitations of their own worldviews and actively seek collaborations to increase the scale and/or sustainability of rewilding application. Given the multiple barriers to genuine collaboration highlighted in the data and elsewhere (Martin et al., 2023), further practical guidance to promote genuine collaboration and inclusion at various scales, and to address institutional biases, are required.

3.1.9 Rewilding is nature-led, human-enabled

There is a clear desire for rewilding to furnish other-than-human nature with the freedom and function to look after itself (Prior and Ward, 2016; Carver et al., 2021; Hawkins, 2022). However, it is also agreed that rewilding application requires some level of human influence, as action and intervention are integral to rewilding practice, as is reflected throughout this paper. This has caused a perceived paradox between the rewilding goal for non-human autonomy and human intervention (e.g., Cózar-Escalante, 2019; Dandy and Wynne-Jones, 2019; Deary and Warren, 2019; Sweeney et al., 2019; Holmes et al., 2020; Wynne-Jones et al., 2020), with conflicting ideas over the amount of human influence compatible with wildness or within rewilding practice. It is this reason that this guideline is included, even though it is strongly linked to other suggested guidelines. Adding to the confusion, human influence or interventions can be seen as controlling of some ecological processes (e.g., induced burning to suppress natural succession), while also being used in rewilding to emulate ecological processes (e.g., induced burning to mimic natural disturbance). Rewilding seeks to improve ecological function and the capacity for ecosystems to be self-sustaining by "giving nature a helping hand" (as reflected in the RPS data). However, the conflict between intervention and autonomy is evident in this statement. Rewilding application therefore requires a balance of ecological knowledge and evidence (linked to section 3.1.7) and humility – acknowledging limits to human understanding of complex ecological interactions. Alan Watson Featherstone suggests asking, "What's Nature seeking to do here? That is crucially different from the ethos of human domination. Rewilding is about humility, about stepping back" (Monbiot, 2013, p.105).

To address the perceived conflict, this guideline suggests that rewilding is nature led, human enabled. Addressing ongoing discussion over the similarities and differences between the fields of ecological restoration and rewilding (du Toit and Pettorelli, 2019; Nelson, 2022), this suggests that one difference may be that ecological restoration is human led, nature enabled, while rewilding is nature led, human enabled. That is to say that approaches in ecological restoration tend to focus on using natural processes and nature-based solutions (e.g. natural flood management) to achieve desired goals or end states as determined by written management plans, whereas rewilding is us, as humans, giving nature the space and the time to determine its own trajectories and outcomes.

3.2 Interventions used in rewilding

While an aim of rewilding is to reduce the need for continued management by enhancing the sustainability and resilience of wild systems (Hawkins, 2022), the data and wider literature reflect that rewilding often entails active intervention. Here we provide a list of interventions associated with rewilding extracted from the data, either those that are suggested or that have been applied. As far as we know, this is the first broad-scale study to provide a list of interventions used in rewilding. These are listed in Table 1 which considers the actions associated with each intervention and their potential for contributing to rewilding aims (as presented in Hawkins et al., in prep.). Relevant projects and existing guidelines are also included, for reference, however this is not a comprehensive list. This table provides a useful tool to inform rewilding practice and can be used as a starting point for planning. However, due to the constraints of this study, the table draws on a limited data set and so further work on this is warranted to inform the ongoing development of IUCN guidelines for rewilding. As rewilding is contextual (as discussed in section 3.1.3) the interventions may not be suitable in all contexts and there may be other suitable interventions that are not listed here.

A key point to note is that this table demonstrates that rewilding uses a suite of interventions in pursuit of rewilding aims, it is therefore more than one intervention or more than the sum of its parts. This can help to encourage more place-based, holistic thinking in rewilding, addressing tendencies to equate rewilding with an intervention, e.g., reintroductions, grazing, or wilderness – perceptions which can cause conflict among rewilding proponents, as reflected in the data. As Table 1 demonstrates, interventions that are highlighted in the data relate both to ecological restoration and socio-cultural change. This further reflects the transdisciplinarity of rewilding (Hawkins et al., 2022). It should also be noted that the data reflect that rewilding can happen without any intervention, through spontaneous rewilding or natural recolonisation (McKibben, 1995; Boitani and Linnell, 2015; Navarro and Pereira, 2015a; Carver, 2019), for example due to land abandonment. As this involves no direct conscious choice or intervention, this is not listed as an intervention in Table 1, but it must be noted that ecological processes continue, develop, or change where they are given the opportunity to do so. Spontaneous responses to the (unintended or intended) removal of human influence has had significant influence on rewilding theory and practice (McKibben, 1995; Carver, 2019; Locquet and Carver, 2022), and future examples may continue to provide guidance for if, how, and when to intervene.

Table 1 demonstrates potential conflicts between rewilding interventions. For example, interventions to promote connectivity can include removing fencing (Foreman, 2004), while fencing is also used to limit unwanted herbivory (Ashmole and Chalmers, 2004; Featherstone, 2004) and to limit the movement of reintroduced animals (Taylor, 2008). Another conflict noted is between interventions that seek to limit successional processes [which include introducing wild, de-domesticated, or domestic grazers, burning, or cutting (Navarro et al., 2015; Svenning et al., 2016)] and interventions that seek to promote succession and afforestation, including limiting over grazing and over browsing by wild or domestic animals (Ashmole and Chalmers, 2004; Featherstone, 2004). This reflects the conflict between herbivore-focused rewilding and afforestation noted in the data (e.g., Fenton et al., 2004; Sandom and Wynne-Jones, 2019). Variations in the perceptions or roles of non-native species are also noted, i.e., the use of ecological surrogates and the lethal control of non-native invasive species, both to aid rewilding (Sandom et al., 2013; Cidrás and Paül, 2022). These conflicts highlight the difficulty in achieving natural autonomy or total withdrawal of human influence, with human preferences influencing practice and ongoing intervention needed to address perceived ecological inadequacies, such as a lack of habitat, missing species, or non-native species. Rewilding principles (Carver et al., 2021) and the guidelines presented here are intended to guide the planning and prioritisation of interventions, but personal or stakeholder preferences and priorities continue to influence rewilding (Sandom and Wynne-Jones, 2019; Holmes et al., 2020). There is a question over whether rewilding should be flexible and allow for "creative pluralism" (Deary and Warren, 2019). This is reflected in the intention for rewilding to be contextual and place-based (section 3.1.3) and adaptable (section 3.1.6). Table 1 may help practitioners to consider a wide suite of interventions to encourage creative pluralism and respond to contextual factors, rather than to approach rewilding with pre-conceived ideas of which interventions to apply.

3.3 Rewilding theory of change framework

The results of the analysis of the RPS and IRT data led to the construction of a proposed ToC framework which is aimed at practitioners, encouraging the construction of adaptive, place-based

TABLE 1 A list of interventions that are associated with rewilding as extracted from the RPS and IRT data, demonstrating how these are intended to contribute to rewilding aims and the actions that are associated with these interventions. Related projects and guidance are suggested for further reference.

Interventions	Contributions to rewilding aims[1]	Actions associated with intervention	Project examples and relevant guidance[2]
Protected areas: restoring or repurposing existing protected areas or establishing new protected areas	To protect areas (of land or sea) from unsustainable human activities, to promote natural autonomy or other ecological aims of rewilding, forming core areas of regional network designs, and contributing to achieving other rewilding aims. The different protected area categories are noted (Johns, 2019; IUCN WCPA) and how each relates to rewilding is a topic for future research.	• Purchasing, reallocating, or legally protecting areas of land to create protected areas for rewilding. • Engaging existing private landowners, managers, communities, or other relevant stakeholders/decision makers to promote protection of areas for nature and rewilding, including restoration or improvements of existing protected areas. • Engage landowners, managers, communities, or other relevant stakeholders/decisionmakers to restrict development, exploitation, or activities that cause ongoing ecological degradation. • Limit access or certain types of use, for example through fencing, signage, or law enforcement.	• IUCN WCPA guidelines for protected areas and other guidance (Noss et al., 1999; Carruthers-Jones et al., 2022; IUCN WCPA) • Rewilding Argentina (Pettersson and de Carvalho, 2021; Donadio et al., 2022) • Trees for Life, Scotland (Featherstone, 2004) • Carrifran Wildwood, Scotland (Ashmole and Chalmers, 2004; Adair and Ashmole, 2022) • Gorongosa National Park, Mozambique (Pringle, 2017; Pringle and Goncalves, 2022) • Terai Arc Landscape, Nepal/India (Ram Bhandari and Raj Bhatta, 2022).
Connectivity, corridors, and buffers	Expand habitat to accommodate nature around or between existing areas of habitat or protected areas, promoting connectivity, natural autonomy, and coexistence.	• Remove barriers to natural processes, especially dispersal, e.g., fencing, dams, or reducing anthropogenic disturbance. • Constructing wildlife bridges or underpasses. • Engaging with stakeholders in target areas to influence land use decisions. • Mitigating human-wildlife conflict in target areas, including engagement to promote coexistence. • Restoration of habitat in target areas. • Identifying opportunities for corridors, e.g., riparian zones, and influence land use in target areas. See landscape mapping.	• Connectivity guidance (Dobson et al., 1999; Hilty et al., 2020; Carruthers-Jones et al., 2022) • Yellowstone to Yukon, US/Canada (Hilty et al., 2022, 2024) • Affric Highlands, Scotland (Trees for Life) • Weald to Waves, England (Weald to Waves) • Terai Arc Landscape, Nepal/India (Ram Bhandari and Raj Bhatta, 2022).
Regional network designs and landscape mapping	To provide top-down influence on policy and land-use decisions in target areas, improve ecological knowledge, encourage landscape-scale approaches, and contribute to monitoring.	• Creating maps to monitor change and identify opportunities and barriers to rewilding or natural movement. • Using maps to engage with stakeholders in target areas to influence land use decisions. • Promote other rewilding interventions in target areas. • Promote collaboration and networking across target areas.	• Guidance for opportunity mapping (Ceausu et al., 2015; Zoderer et al., 2019; Carver, 2022) • The Wildlands Network, US (Soulé and Terborgh, 1999a; Foreman, 2004, 2004) • Yellowstone to Yukon, US/Canada (Hilty et al., 2024).
Restoration of habitat, natural disturbance, and/or natural succession	Restoring ecological structure, function, and heterogeneity based on reference ecosystem or conditions; accommodating nature; improving human-nature or human-place connection and provision of ecosystem services. Includes a wide range of habitats including marine, coastal, wetland, riparian, soil.	• Reintroduce fauna that can contribute to natural regeneration, improving and maintaining habitat, e.g., apex predators to limit grazing pressure, beavers to improve riparian habitats, herbivores to limit succession, or seed dispersers. • Planting of trees and shrubs (can include seed collection and propagation). • Remove barriers to natural regeneration or disturbance, e.g., reduce mowing; reducing anthropogenic disturbance; reducing grazing using fencing, culling, or grazing reform. • Interventions to promote or imitate natural disturbance or limit succession, e.g., prescribed burning, grazing. • Removal or thinning of non-native invasive or dominant species, e.g., sitka spruce in areas that were previously used in commercial forestry. • Promoting habitat restoration or natural disturbance to landowners, users, or managers. • Protecting areas where natural disturbance or habitat does not conflict with human land use.	• Guidance on habitat restoration via reintroduction (Barlow, 2000; Sandom et al., 2013; Svenning et al., 2016; Bakker and Svenning, 2018) • Guidance on habitat restoration (Soule and Noss, 1998; Simberloff et al., 1999; Merckx, 2015) • Trees for Life, Scotland (Featherstone, 2004) • Carrifran Wildwood, Scotland (Adair and Ashmole, 2022) • Gelderse Poort, the Netherlands (Jepson et al., 2018) • Wild Ennerdale, England (Browning and Yanik, 2006) • Rangelands Restoration, Australia (Kealley and Burrows, 2022) • Terai Arc Landscape, Nepal/India (Ram Bhandari and Raj Bhatta, 2022).

(Continued)

TABLE 1 Continued

Interventions	Contributions to rewilding aims[1]	Actions associated with intervention	Project examples and relevant guidance[2]
Species reintroduction or conservation introduction	To promote the recovery of viable populations of extirpated species, restore their ecological function, to achieve ecological aims of rewilding and contribute to other rewilding aims. Where missing species are extinct, ecological surrogates can be considered for introduction, to fulfil the ecological roles of extinct species.	• Missing species assessments to clarify which species are missing, and an understanding of their ecological roles or cultural value to aid prioritisation, i.e., as keystone, highly interactive, umbrella, or culturally significant species. • Ecological and social feasibility studies. • Reintroductions of locally extirpated species or, where necessary, introductions of ecological surrogates to fulfil the ecological roles of extinct species [following the IUCN (2013) "guidelines for reintroductions and other conservation translocations" or other local or international legal requirements (see Eagle et al., 2022)]. • Ongoing monitoring to understand ecological, social, economic impacts of translocations. • Mitigate risk of human-wildlife conflict, e.g., fencing to limit the movement of reintroduced species or limit access by humans; ongoing engagement and consultation.	• Guidance and guidelines for (re) introductions (IUCN, 2013; Bakker and Svenning, 2018; Seddon and Armstrong, 2019; Stanley-Price, 2022) • Rewilding Argentina (Donadio et al., 2022) • Rangeland Restoration, Australia (Kealley and Burrows, 2022) • beaver reintroductions, UK (Gow, 2006, 2011; Prior and Ward, 2016; Jones and Jones, 2023) • guanaco reintroductions, Chile (Lindon and Root-Bernstein, 2015).
Management of invasive or dominant species	To reduce over-dominant species or remove invasive non-native species that hinder progress of rewilding or related interventions.	• Prioritise the removal or management of dominant or invasive species based on their potential to hinder rewilding or to disperse or to control regionally (would need to be controlled everywhere to be effective). • Assess different methods of control. • Remove or reduce number of invasive or dominant species, e.g., thinning of sitka spruce plantations; removing invasive eucalyptus; culling or deer fencing. • Reintroduce species that may contribute to managing the number or movement of dominant or invasive species. • Promote reduction of stocking densities of domestic livestock, or grazing reform. • Raise awareness of the impacts of domestic, dominant, or invasive species on ecological function. • Prevent the introduction of invasive species, e.g., limiting access, targeting policy on wildlife trade, raising awareness.	• Guidance on invasive species management in rewilding (Simberloff et al., 1999; Kirby et al., 2004; Sandom et al., 2013; Sweeney et al., 2019; Cidrás and Paül, 2022) • Trees for Life (Featherstone, 2004) • Carrifran Wildwood (Ashmole and Chalmers, 2004; Adair and Ashmole, 2022) • Rangelands Restoration, Australia (Kealley and Burrows, 2022) • Fragas do Eume Natural Park, Spain (Cidrás and Paül, 2022) • Wild Ennerdale (Browning and Yanik, 2006).
Mitigating human-wildlife conflict	To enhance potential for coexistence and human tolerance, avoid lethal control of species, and promote natural autonomy.	• Implementing strategies to mitigate conflict, including traditional methods (such as shepherding), modern techniques (e.g., electric fences, green fences, livestock protection collars, GPS tracking of predators), or reform of hunting quotas. • Translocation or lethal control of animals where they are negatively impacting coexistence and tolerance. • Providing compensation for loss of crops, livestock etc, or incentives for implementing mitigation strategies. • Public and policy engagement promoting coexistence, legal protection, mitigating SBS, and improving tolerance and willingness to obey laws and restrictions. To understand local motivations for persecution and mitigate these risks. • Land-use zoning or planning or influencing the distribution of human activities at a landscape scale to reduce potential conflict. Promoting corridors, connectivity, and buffer	• Guidance on coexistence in rewilding context (Boitani and Linnell, 2015; Carter and Linnell, 2016; Linnell and Jackson, 2019; Lambert and Berger, 2022) • wild boar coexistence, England (Gow, 2002; Goulding, 2004, 2008) • Andhari Tiger Reserve, India (Johns, 2019) • lynx reintroductions, Europe (von Arx and Breitenmoser, 2004) • Velebit Mountains, Croatia (Jepson et al., 2018) • wolves in the French Alps (Bennett, 2006) • bears in Austria (Rauer, 2004).

(Continued)

TABLE 1 Continued

Interventions	Contributions to rewilding aims[1]	Actions associated with intervention	Project examples and relevant guidance[2]
		zones especially where there is likely to be high conflict.	
Networking and knowledge sharing	Promoting collaboration of rewilding organisations or projects to share learning, extend area for rewilding, and increase influence. Improve the sustainability of results of rewilding. Foster trust, collaboration, and best practice.	• Creating maps or lists of projects and organisations working in areas to promote collaboration, partnerships, and connectivity. • Seeking and encouraging collaborations across different organisations, land managers, policy makers, researchers, disciplines etc. • Aligning visions or aims across rewilding projects. • Sharing knowledge and experiences, e.g., through webinars or publications. • Communication and transparency of organisational/project aims. • Communication of research requirements to promote collaboration with researchers.	• Rewilding Europe (Helmer et al., 2015; Jepson et al., 2018) • Rewilding Britain (Rewilding Britain) • the wildlands network group, UK (Taylor, 2011) • Rewilding Institute (Foreman, 2008) • Wildlands Network (Foreman et al., 1992; M. E. Soule and Terborgh, 1999a) • Tweed Forum (Comins, 2004).
Promoting or implementing sustainable land management or resource use	Improving habitat and increasing autonomous nature (usually in traditionally anthropogenic areas, e.g., agricultural, commercial forestry, or urban areas), preventing overexploitation, and limiting unsustainable activities to promote connectivity and coexistence.	• Implementing or promoting regenerative or wildlife-friendly farming, including restoring habitat such as hedges or field margins, reforming livestock grazing, ending the use of insecticides, or diversifying crops/polyculture. • Implementing or promoting reforms to commercial forestry, including ending clear-cutting, selective logging, sustained yield, limiting heavy machinery, increasing species and age diversity in commercial forests, and promoting local use of timber. • Promoting the reform of mining or other extractive practices. • Legal species protections, no-take zones (or protected areas), or limitations to hunting or foraging. • Improving habitat, promoting natural autonomy, or rewilding in urban areas. • Providing or promoting incentives to encourage landowners or managers to restore habitat or accommodate nature, e.g. through compensation schemes for losses caused by natural disturbance or predation or payments for ecosystem services provided by habitat restoration. • Limiting recreational access or other activities to areas when it may negatively impact natural processes, e.g., during nesting season, when there is risk of disease spreading, or when paths are being degraded through overuse. • Public engagement to improve ecological knowledge and raise awareness to promote responsible use of land or resources. • Promoting the reform of policies that promote intensive agriculture or other unsustainable activities.	• Sustainable land use guidance/proposals (McKibben, 1995; Groom et al., 1999; Fisher, 2004; Benayas and Bullock, 2015; Merckx, 2015) • urban rewilding (Maller et al., 2019; Owens and Wolch, 2019) • proposed policy reform (Kirby et al., 2004; Pettorelli et al., 2018) • Knepp Wildland, England (Taylor, 2006; Tree, 2019) • Neroche, England (Saunders, 2011) • Tweed Rivers Heritage Project (Comins, 2004) • Rewilding Europe (Helmer et al., 2015; Jepson et al., 2018).
Public engagement and education	Generally promoting rewilding and its aims, and involvement in projects. Aims to improve ecological knowledge and human-nature connection, mitigate SBS, encourage or inform people to better accommodate or coexist with nature in landscapes, and ultimately (re) integrating nature into culture.	• Use of cultural heritage or the arts to raise awareness of missing species or to achieve other rewilding objectives, e.g., through sharing folk music, storytelling, popular fiction or non-fiction books, spiritual practices, or traditional skills. • Demonstrating sustainable practices or ecocentric cultures, for example sharing the values or practices of indigenous cultures or anarcho-primitivism. • Promoting or offering (sustainable) nature experiences, e.g., nature walks, ecotourism,	• Guidance for community conservation and involvement (RARE, 2014; Charles, 2021; Weber Hertel and Luther, 2023) • Terai Arc Landscape, Nepal/India (Ram Bhandari and Raj Bhatta, 2022) • Yellowstone to Yukon, US/Canada (Hilty et al., 2022) • community nature conservancies (Johns, 2019) • Abbots Hall, England (May et al., 2006) • beaver reintroduction, Scotland (Prior and Ward, 2016)

(Continued)

TABLE 1 Continued

Interventions	Contributions to rewilding aims[1]	Actions associated with intervention	Project examples and relevant guidance[2]
		safari-style experiences, forest schools, or outdoor education and play. • Informational signage in rewilding or nature areas to educate and raise awareness. • Advocating for rewilding in local, national, or global policy. Promoting the benefits of rewilding to societal wellbeing and assisting the public to benefit from rewilding-related incentives. • Promoting ecological science and improving ecological knowledge through science communications. • Involving communities or other stakeholders in rewilding, for example through volunteering, consultation, advisory groups, or citizen science.	• Neroche, England (Saunders, 2011) • Moor Trees, England (Griffin, 2004).
Monitoring	Improve knowledge of the impacts of rewilding interventions, share learning and promote best practice, feed into adaptive planning (linked to section 3.1.7).	• Setting project goals which will provide a basis for monitoring. Establish ecological reference ecosystem for monitoring ecological progress, e.g., historical or palaeoecological evidence. • Determine needs of focal species/ecological processes. • Setting up monitoring programmes appropriate to available resources, ensuring that these are sustainable over time. • Look for potential areas to act as comparison areas where no rewilding action is taken, e.g. neighbouring land (Ashmole and Chalmers, 2004) or exclosures (Bakker and Svenning, 2018).	• Guidance for monitoring rewilding (Groom et al., 1999; Corlett, 2019; Beyers and Sinclair, 2022; Root-Bernstein, 2022) • Natural Capital Laboratory at Birchfield, Scotland (White et al., 2022) • Carrifran Wildwood, Scotland (Adair and Ashmole, 2022) • Abbots Hall, England (May et al., 2006) • Hafod y Llan, Wales (Neale, 2004) • monitoring of bears in Austria (Rauer, 2004) • Wicken Fen, England (Warrington et al., 2009).
Securing and managing funding or other resources for rewilding	To support the economic viability and sustainability of rewilding (to support long-term viability as discussed in section 3.1.4).	• Securing public or private funding for rewilding, e.g., crowd funding, charitable donations, philanthropists, government funding, legacy donations. • Securing land for rewilding, e.g., legacy donations, landowner agreements. • Promoting policy to incentivize restoration or rewilding or to encourage charitable donations, e.g., payments for ecosystem services, agri-environment schemes, tax relief, carbon tax credits. • Using natural capital accounting to demonstrate the value of ecosystem services to promote incentives. • Integrating funding for rewilding into rewilding practice or promoting sustainable livelihoods as part of rewilding, e.g., income from ecotourism or recreational activities, income from breeding of animals or plant nurseries for rewilding, Community Nature Conservancies (Johns, 2019). • Establishing central funding resources to facilitate green investments for rewilding. • Promoting projects to secure volunteer time. • Gaining awareness of and utilising existing potential funding streams, e.g., European Commission Natural Capital Financing Facility, Forestry Commission Woodland Grant Scheme, Scottish Forestry Grants Scheme, Heritage Lottery Fund. • Establishing compensation funds.	• Rewilding Europe Capital (Rewilding Europe) • Carrifran Wildwood, Scotland (Ashmole and Chalmers, 2004) • Tweed Rivers Heritage Project (Comins, 2004) • Great Bustard reintroduction, England (Dawes, 2006) • Mar Lodge, Scotland (Holden and Clunas, 2004) • several projects led by Rewilding Europe (Jepson et al., 2018) • Neroche, England (Saunders, 2011).

[1]As described in Hawkins et al. (in prep.; after Hawkins, 2022, 2023).
[2]This column has been extracted from the data, other known projects, and guidelines. Given the limitations of this study, the projects and guidelines referenced are based on limited sources and a more thorough review of the literature and case studies for each intervention could be done in future to improve the table.

ToCs (Figure 2). This ToC framework integrates the guidelines from section 3.1, providing further guidance on when and how to address these in project planning. This ToC framework to inform rewilding application is adaptable to different contexts. The purpose of each stage is outlined below, while the rewilding vision included in the figure refers to rewilding aims established by Hawkins (2022) and Hawkins (2023).

3.3.1 Stage 1: vision and outcomes

A defining principle of a ToC is that a vision for the future related to the intended change is created to provide a focus for the project or organisation (Reinholz and Andrews, 2020; Centre for Theory of Change). This is related to the intention for rewilding to be transformative and visionary (section 3.1.1). As such, the social-ecological aims of rewilding (Hawkins, 2022; Figure 2) can be used as a template from which to adapt a context-specific rewilding vision that represents what is ultimately to be achieved. Here those driving rewilding are asked to reflect on their intentions and are encouraged to think long term and systemically, as reflected in the above guidelines, considering the ecological, socio-cultural, and systemic change required to achieve their vision. Following the creation of the vision, outcomes can be identified, which are the pre-conditions or qualities that are needed to achieve the vision (Figure 1). These qualities can serve as measurable indicators to monitor the impacts of rewilding application.

3.3.2 Stage 2: contextual assessments

Reflecting intentions for rewilding to be contextual and place-based, the second stage entails a thorough assessment of social and ecological conditions in the focal area or system. This would include the drivers of change and specific needs, problems, or barriers to address. These consider historic land use and conditions related to ecological and socio-cultural factors and so would encourage interdisciplinary collaborations (section 3.1.8) and systems thinking (section 3.1.5). This stage may also include the identification of opportunities and resources available, such as available land or sources of funding. This stage encourages projects to assess the conditions to inform rewilding plans, rather than adopting approaches or imitating other rewilding projects, that were developed in other contexts.

This stage is critical for creating the evidence required to inform rewilding plans and establish ongoing monitoring (section 3.1.7); it integrates monitoring into rewilding, a crucially important step towards improving rewilding application and to inform rewilding policy and guidelines. In the first iteration of a project, the assessment would provide a baseline while further iterations would monitor change over time. As is identified in section 3.1.7, there is a need to develop clear guidance for monitoring. In the absence of such guidance, Table 1 provides some examples of monitoring in rewilding projects and some guidance from the literature.

3.3.3 Stage 3: selecting, prioritising, and applying interventions

Based on the above assessments, a list of potential interventions can be created. These would ideally look to take advantage of opportunities and work to overcome barriers identified in stage 2. Table 1 demonstrates the variety of interventions used in rewilding and can be used to inform the selection of interventions, although there may be other suitable interventions that are not reflected in this list. This list also includes related guidance to improve the effectiveness of these interventions, but wider evidence to inform interventions should be considered given the limitations to this table.

The initial list of potential interventions must then be prioritised based on current feasibility, aligning with intentions for rewilding application to be contextual and pragmatic. Interventions that are most feasible are prioritised, recognising their potential to enhance the feasibility of other intended interventions. As an example, in the Rangelands Restoration project in Australia, non-native species have been identified as a major barrier to rewilding and therefore non-native species management has been prioritised over species reintroductions

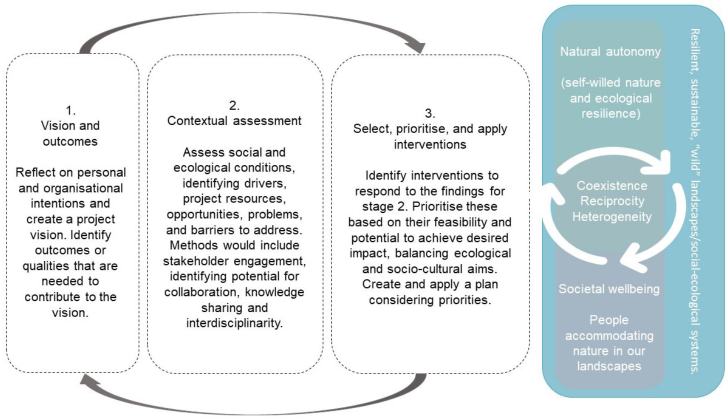

FIGURE 2
A proposed rewilding ToC framework to inform rewilding application. An earlier version of this framework, based on the RPS data, was published in Hawkins (2022).

(Kealley and Burrows, 2022). As interventions are prioritised, they provide the basis to map steps from the present context to the desired future, as is encouraged by a ToC framework (Figure 1). High priority interventions are then applied first, and others applied successively. Considering the example of Carrifran Wildwood (Adair and Ashmole, 2022), priority interventions included seeking funding and purchasing land, these were followed by interventions to address barriers to habitat restoration (removing grazing sheep, constructing deer fencing, and culling of deer), followed by interventions to restore habitat (seed propagation, sourcing of saplings, tree planting). Application should consider existing guidelines for each intervention to ensure that these are applied ethically and effectively (informed by Table 1 and other existing guidance). Depending on the scale of the project and resources available, several interventions may be applied simultaneously, and the time scale of this stage will depend on the complexity of the project and the interventions applied.

3.3.4 Successive iterations

Reflecting agile project management (Fernandez and Fernandez, 2008) and the adaptive governance framework for rewilding identified in the literature (Butler et al., 2021), stages 1–3 are repeated iteratively. Hence the project goals, project context, and application are reassessed, and plans updated in an adaptive approach. This allows ongoing monitoring of change and effectiveness of interventions which will contribute to the growing rewilding knowledge base. ToC iterations are critical as they encompass the adaptability and uncertainty (section 3.1.6) inherent in rewilding. Rewilding remains adaptable, as in reality projects are likely to adapt plans around emerging opportunities or barriers that were not identified in stage 2. Rewilding application is unlikely to be as linear as suggested by this framework, but it provides a useful tool to guide application nonetheless.

Reflecting intentions for rewilding to be inclusive and collaborative (section 3.1.8), project leaders will need to consider who to include in decision making and project governance related to each stage. Some interventions listed in Table 1 are done with the aim of promoting inclusion and collaboration, including networking and knowledge sharing which are promoted by organisations including Rewilding Europe, Rewilding Britain, and the Rewilding Institute. Given the iterative nature of this framework, who is included in decision making can be adapted depending on the progress of the project or the resources available. Smaller projects with limited resources and space, or existing projects which have not previously identified as rewilding projects, are encouraged to embrace systems thinking and consider several aims and outcomes as part of the rewilding vision suggested by this framework. They can adapt plans as opportunities arise to extend the area and/or impact of their project. Examples of two projects highlighted in Table 1 can help to demonstrate how the ToC can be adapted to suit different scales or to different priorities or resources. Firstly, Hilty et al. (2022) demonstrate that a large-scale rewilding vision (stage 1) was critical for the Yellowstone to Yukon project. This organisation does not own any land and interventions relate to engaging with people to influence land use or management decisions over a large spatial scale to promote connectivity and coexistence. In contrast, Adair and Ashmole (2022) demonstrate how even small-scale projects can expand their aims over time. Carrifran Wildwood initially focused funding and ecological restoration to achieve a rewilding vision, but later sought to expand the influence and impact of the project beyond the original spatial boundary by approaching local landowners and forming collaborations.

4 Conclusion

This article seeks to highlight the diversity of interventions available to rewilding practitioners to promote creativity and dynamism in application, while the guidance drawn from the data promotes more holistic thinking and paradigm shifts in the culture of rewilding practice. In many cases, rewilding is still driven by human decision making and individual preference. There is inherent difficulty in applying rewilding, as we continue working with (our own or others') extant values and assumptions while promoting transformative change. For example, Wynne-Jones et al. (2020) note that metrics used to measure or plan for rewilding are still denominated by benefits for humans, which is a barrier to integrating notions of intrinsic value and ecocentrism. Martin et al. (2023) show that, despite aspirations and commitments for rewilding to be inclusive, genuine collaboration is limited by entrenched views of power, ownership, and tendencies to prioritise one's own interests. While rewilding may seek to be inclusive, it also looks to counteract root causes of ecological degradation, many of which are cultural (Maffey and Arts, 2022), and so there is uncertainty reflected in the data and wider literature over how to balance promoting cultural change with respect for people's extant values (Hawkins et al., 2020; Root-Bernstein, 2022). Notions of equity may help to promote equitable routes to system sustainability, as are reflected by circular economics (UNDP), systems thinking (section 3.1.5, Fougères et al., 2022), and the social-ecological aims of rewilding (Hawkins, 2022.). In this framing, change is justified as it is promoted in pursuit of equity, holistic wellbeing, and SES sustainability and resilience. This approach promotes collaboration in the pursuit of a shared vision. In this sense rewilders ideally become facilitators promoting change and encouraging collaboration across the more than human community.

The literature also highlights some key issues that may serve as barriers to realising the desired paradigm shifts in rewilding practice, or its transformative goals. These include dualistic ontologies that drive commodification of natural resources (Irwin, 2021), anthropocentrism (Wynne-Jones et al., 2020), and continued compartmentalisation of human and non-human nature (Cózar-Escalante, 2019); scientific rationalism and intolerance for risk and uncertainty; and tendencies to limit project areas to avoid social-ecological complexity, limit dispute, and maintain control over rewilding application (Wynne-Jones et al., 2020; Martin et al., 2023). Desired qualities that are promoted in response to these barriers include more holistic or ecocentric worldviews that expand notions of wellbeing and interests to more-than-human nature (Cózar-Escalante, 2019; Wynne-Jones et al., 2020; Irwin, 2021); improved adaptiveness and tolerance for uncertainty and dynamism inherent in wilder systems (Cózar-Escalante, 2019; Holmes et al., 2020); and genuine collaboration, trust, and empowerment among stakeholders (Pettersson and de Carvalho, 2021; Martin et al., 2023). While there are a range of legitimate concerns about compromise, the literature also suggests that there is the potential for rewilding to be both pragmatic and visionary. For example, Pettersson and de Carvalho (2021), in their study of rewilding at Iberá National Park, note a need to continually balance pragmatic legitimacy (meeting the direct needs or interests of stakeholders) and output legitimacy (delivering milestones and communicating success related to the rewilding vision). Holmes et al. (2020) discuss the possibility for rewilding projects to adapt to socio-cultural contexts, with the potential to balance pragmatism with transformative goals over time, however they highlight that this requires further investigation. The framework presented here in Figure 2 offers a route to balancing transformation with pragmatism.

However, the above demonstrates that while rewilding is intent on outwardly shifting paradigms, i.e., in wider society, much of the work needs to be done inwardly, focusing on the paradigms and institutions within the culture of conservation, restoration, and rewilding, and the suggested guidelines presented here encourage these shifts in rewilding application. This is also important when considering the RTG's work towards guidelines for rewilding and some of the limitations inherent in research and policy environments. One of the barriers to maintaining adaptability is that published guidelines themselves are usually limited by time and resources and are fixed for a certain time rather than adaptable. In this time of uncertainty, it may be prudent to consider the adaptability of published guidelines and frameworks. Part of the process of "rewilding" the culture and practice of rewilding will need to include long-term commitments to adaptable approaches to rewilding that focus on finding place-based responses to dewilding and ecological degradation. This means that projects must adapt around social-ecological assessments of rewilding areas to inform plans, rather than approaching rewilding with pre-conceived ideas of what interventions to use. The guidelines highlighted in this article ask those driving rewilding to consider their own intentions and consider themselves as part of the systems within which they are operating, rather than as external and temporary "experts". Barriers to incorporating these principles into practice are highlighted, for example many of the institutions that inform and influence rewilding, such as funding mechanisms, are not adaptable or long-term. In this sense, long-term commitments to achieving rewilding aims are needed, along with longitudinal studies to understand what contributes to the success or failure of rewilding projects.

The tools presented in this paper – guidelines, list of interventions, and ToC – are based on a limited data set and will therefore require testing against global rewilding theory and policy and in case studies of rewilding application to improve their usability and adaptability to different contexts. Despite these limitations, they provide a useful and evidence-based starting point for unifying rewilding policy and practice and a focal point for identifying areas requiring further research or refinement. The framework and the findings presented here encourage the rewilding community to work towards common goals, to adopt complex systems thinking considering social-ecological interactions, and to collaborate and share experiences and lessons learned across systems, cultures, and disciplines to enhance the potential for rewilding. While the framework proposed in Figure 2 is aimed at rewilding practitioners who are looking to apply rewilding interventions on the ground, if we truly intend to effect transformational change, we must also look more widely at the systems and institutions in which rewilding research and practice operates (Fougères et al., 2022). If rewilding is to be a global undertaking, and if it truly has the potential to create transformational change, it must embrace and encourage change across the multiple systems that affect it. Time will tell whether rewilding will affect a virtuous cycle and paradigm shift towards more systemic ways of thinking about rewilding application, embracing uncertainty and indeterminacy, and releasing expectations over the outcomes of rewilding.

Data availability statement

The datasets presented in this article cannot be publicly shared due to privacy restrictions. Requests to access the datasets should be directed to the corresponding author.

Ethics statement

The studies involving humans were approved by University of Cumbria ethics committee. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

SH: Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. IC: Writing – review & editing, Supervision, Conceptualization. SC: Writing – review & editing, Supervision, Conceptualization.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1384267/full#supplementary-material

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Reflooding the coupled human and natural system of the Waza-Logone Floodplain, Cameroon

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The rewilding framework is used to guide the restoration of ecological processes in natural systems, but the framework can also be used in the restoration of social and ecological processes in coupled human and natural systems. We use the case of the large-scale reflooding of the Waza-Logone Floodplain in Cameroon three decades ago as an example of rewilding a coupled human and natural system. Drawing on studies that have been conducted of the Logone Floodplain and Waza National Park over the last five decades, we discuss the reflooding efforts, review the long-term impact of the reflooding, and reflect on the assumptions of the reflooding effort. Our review shows that restoring the hydrological and ecological processes benefitted human populations but was not sufficient for supporting wildlife; and, political dynamics impact ecological processes and must be considered for rewilding to succeed.

KEYWORDS

rewilding, reflooding, social-ecological processes, coupled human and natural systems, vegetation, wildlife, pastoralists, insecurity

Introduction

The reflooding of the Logone Floodplain in the Far North Region of Cameroon three decades ago can be conceptualized as a large-scale abiotic rewilding of a social-ecological system in which humans are an integral part. In our review of this case study, we explore how the frameworks of rewilding and coupled human and natural systems can be integrated to support the restoration of social and ecological processes in floodplains and other social-ecological systems. The case shows how rewilding and restoring ecosystem processes was beneficial for human systems, but that it was not sufficient for protecting wildlife in the floodplain. The lack of involvement and investment of the government in supporting Waza National Park to protect its wildlife may have been one of the main reasons why the reflooding did not benefit wildlife.

The goal of rewilding, according to Carver et al. (2021), is "the restoration of functioning native ecosystems containing the full range of species at all trophic levels while reducing human control and pressures" (1888). The authors outline ten principles for rewilding, which include landscape-scale planning focusing on restoring ecological processes that are always changing, particularly within the context of global climate change (Carver et al., 2021). The rewilding approach makes an analytical distinction between human and natural systems with the goal of separating the two. While it may be possible to reduce human control in some systems (and to reduce natural controls of human systems), that is not necessarily a desirable goal, and it may be counterproductive.

The framework of coupled human and natural systems also makes an analytical distinction between human and natural systems (Liu et al., 2007), but unlike the rewilding approaches it does not seek to separate humans and nature (Figure 1). Rather it views the world as consisting of dynamically coupled human and natural systems, or, better, coupled human and natural *processes*. For example, there are currently no areas that are not affected by humans (e.g., plastic particles at the north pole) and there are no areas in which nature does not shape humans (e.g., antibiotic-resistant bacteria in hospitals). Moreover, these systems are tightly integrated through the couplings between human and natural processes, that can be beneficial (e.g., trees providing ecosystem services in cities, pastoralists creating grazing lawns in savannas) or detrimental (e.g., ticks from deer spreading Lyme's disease in cities, concentrated animal feeding operations polluting streams and rivers). In the framework of coupled human and natural systems, rewilding involves restoring ecological processes that can contribute to equitable and sustainable outcomes for both humans and wildlife.

The main difference between the two frameworks is that the coupled systems framework is relatively agnostic about what the state of these systems should be, as it is foremost an analytical framework, whereas the rewilding framework has a normative component or purpose, which is to restore natural systems by reducing human impacts.

The Waza Logone Project that led the reflooding efforts to restore the coupled human and natural system of the Logone Floodplain aimed to restore ecological processes to contribute to equitable and sustainable outcomes for both humans and wildlife. Rather than reducing human impacts, reflooding the Logone Floodplain was about serving both humans in the Logone Floodplain and wildlife in Waza National Park. In this paper, we discuss these reflooding efforts and their long-term impacts. One of the themes in our discussion is that while the reflooding was a short-term success, the benefits of reflooding were uneven for humans and wildlife in the long-term, mainly because of security problems in the region and lack of government investment in the park.

We have written about the reflooding efforts and its impacts previously (e.g., Moritz et al., 2016; Scholte, 2005), but in this paper, we take a long-term perspective considering the impacts of reflooding on human and natural systems in the floodplain. We realize ours is an unusual example of an abiotic rewilding of a large-scale landscape that was beneficial to floodplain inhabitants, but ultimately less so for wildlife populations. The case study demonstrates that rewilding and restoring ecological processes is not only beneficial to natural systems, but also to human systems. In addition, for rewilding to succeed in benefitting both human and wildlife populations, one has to not only restore ecological

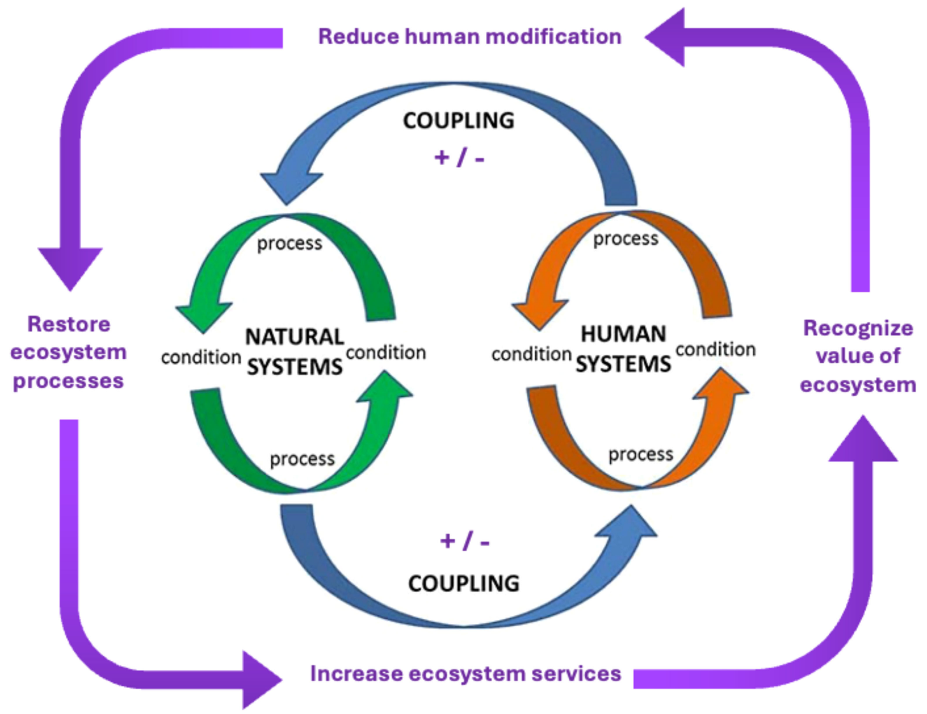

FIGURE 1
Conceptual frameworks of coupled human and natural systems and rewilding. Adaptation of the graphic from the solicitation from the Dynamics of Coupled Natural and Human Systems (CNH) Program at the U.S. National Science Foundation (NSF) (Baerwald et al., 2016). The arrows and text in purple represent the rewilding conceptual framework.

processes, but also consider the social, economic, and political processes that are critical for sustainable development. In some instances, rewilding may benefit from an adaptive co-management approach, which seeks to integrate the social dynamics and priorities of local communities.

Historical context

The Logone Floodplain is located in the Far North Region of Cameroon, and it is one of a number of seasonally flooded flatlands that are an integral part of the watershed of the Chad Basin. It is a key resource area for wildlife, migratory birds, and provides livelihoods for tens of thousands of fishers, farmers, and pastoralists (See Figure 2). The plain is flooded from September through December when the Logone River exceeds 1,500 $m^3 s^{-1}$ (Delclaux et al., 2010), and the area flooded depends directly on the flow rate of the Logone River (Jung et al., 2011). The floodplain is an anthropogenic landscape that has been shaped by human populations for centuries through fishing, herding, and farming (Scholte, 2005). In the last five decades there have been major changes in the flooding regime of the Logone floodplain, with direct and indirect consequences for the coupled human and natural systems of the floodplain. These changes were due to climate change and variability, but mostly due to the engineered modifications of the hydraulic landscape.

A particularly dramatic modification occurred in 1979 when the Cameroonian government embarked on a large-scale infrastructural project to increase domestic rice production in Cameroon. The project involved a 30 km-long dam that created a reservoir – Lake Maga – that was fed by seasonal rivers in the west and by the Logone River upstream of the floodplain. The water in the reservoir is used for irrigated rice fields located north of the dam. To protect the reservoir and rice fields from seasonal flooding, an approximately 50 km-long embankment was built along the west bank of the Logone River (Figure 3). The consequences of these infrastructural projects on the flooding regime were dramatic: large areas in the western part of the floodplain, including Waza National Park, were no longer flooded. As a result of decreased habitat, fish populations declined and many fishermen emigrated or changed their fishing strategies to cope with the decline (Laborde et al., 2016). The reduced flooding also reduced resources and habitats for wildlife and migratory birds in the floodplain (Loth, 2004; Scholte, 2005).

The dam also had major consequences for pastoralists. The reduction in flooding directly affected forage production, in part via a change in plant species composition in areas most affected by the reduced flooding (Scholte, 2005). Perennial species like *Vetiveria nigritana*, *Echinochloa pyramidalis* and *Oryza longistaminata* slowly disappeared, while less palatable annual grasses like *Sorghum arundinaceum* increased in areas where flooding was reduced. Moreover, on the western edge of the floodplain, which no longer flooded, the grass savannah gradually changed into a dense *Acacia seyal* shrubland. Both the shift from perennial to annual species and from grass to woody savannah reduced the grazing resources for pastoralists, many of whom left the floodplain in response (Scholte et al., 2006).

The Waza-Logone Project was an international effort to undo part of the damage of the upstream dam and embankment that severely reduced flooding in an area of 1,500 km^2, including Waza National Park. The project started in 1993 and was based on a decade-long collaboration between the Garoua Wildlife College (Cameroon) and Leiden University (The Netherlands). Earlier unpublished studies of the Logone Floodplain on vegetation, wildlife, fisheries, and pastoralism, showed the impact of the floodplain desiccation, and drew the attention of authorities in Cameroon and the Netherlands. Dutch researchers successfully

FIGURE 2
Livelihoods and wildlife in the Waza-Logone Floodplain. Clockwise from top-left: Korrigum drinking in Waza National Park, fisher navigating the floodplain during the flooding season, herder watering cattle in the dry season (pictures from Paul Scholte and CARPA).

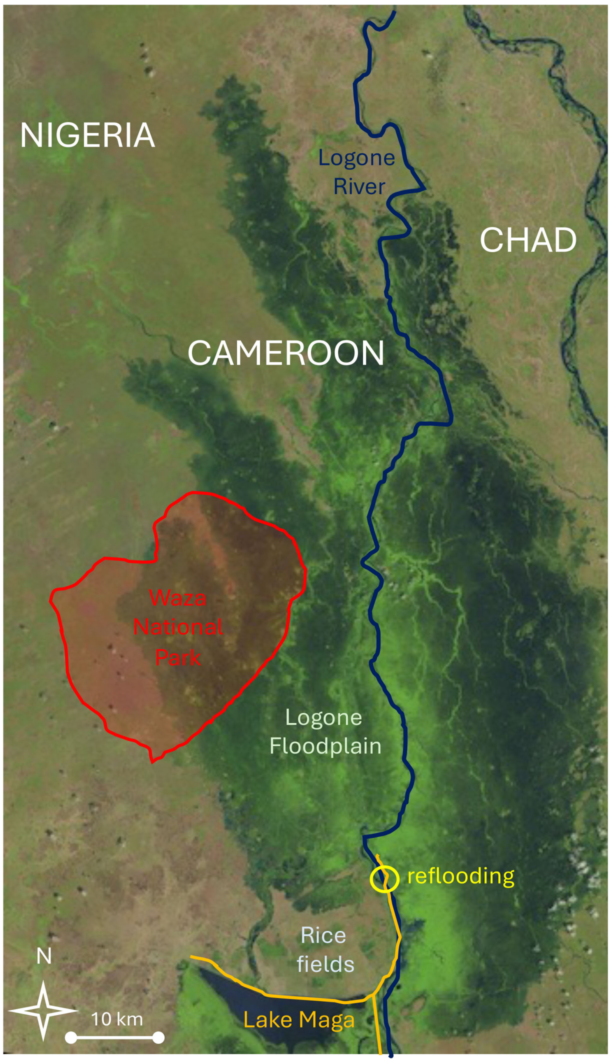

FIGURE 3
Map of the Logone Floodplain. The flooded area is colored green. The yellow circle indicates where the Waza Logone project opened two waterways in the embankment for the reflooding of the floodplain.

lobbied the Netherlands Ministry of Development Cooperation to make funds available for a specifically designed project on floodplain rehabilitation. The International Union for Conservation of Nature and Natural Resources (IUCN) was invited to lead the project, in collaboration with Cameroonian authorities, Leiden University, and the Netherlands Development Organisation (SNV).

The Waza-Logone Project aimed to serve both wildlife in Waza National Park and the human inhabitants of the Logone Floodplain. The researchers appealed to donors through their integrated approach, which focused on rehabilitating both the human and natural systems of the floodplain. They were concerned that reflooding efforts that focused only on the human systems, may generate less interest and funding from donors for the project. For inhabitants of the floodplain, the park and plain are two distinct entities, pastoralists, for example, refer to the floodplain as *yaayre* (floodplain) and the park as *surande* (forbidden area). It is generally conservationists who refer to the area as the Waza-Logone Floodplain to stress the ecological connectivity.

The Waza-Logone reflooding project started off with hydrological studies, showing limited risks to rice fields north of the dam, resulting in recommendations to initiate controlled pilot releases of water with monitoring (Wesseling et al., 1994). The options for reflooding were discussed with local communities and authorities. Their overwhelming positive feedback led to the opening of two watercourses blocked by the embankment. The first was opened in 1994 and the second in 1997, resulting in an additional water flow into the floodplain with a maximum debit of about 20 and 10 m^3/s respectively. Some 600 km^2 of desiccated floodplain have since been reflooded. Over the following three decades, different research teams have monitored how the coupled human and natural systems of the floodplain responded to the reflooding.

Studies of the Logone Floodplain

The human and natural systems of the Logone Floodplain have been studied for six decades, from before dam construction through to the reflooding. These anthropological, ecological, hydrological, and interdisciplinary studies have provided us with a long-term perspective on the dynamics and resilience of this coupled system and its components.

Before the construction of the dam, a range of studies were conducted in the floodplain, including the hydraulics of the floodplain (Billon et al., 1966), fish and fisheries (Bénech and Quensière, 1983; Blache et al., 1962), the vegetation in the Logone Floodplain with a rangeland productivity perspective (Gaston and Dulieu, 1976), a vegetation study of Waza National Park (Wit, 1975), a sociological study of pastoralists and livestock in the Logone Floodplain (Beauvilain, 1979, 1981), and a study of large herbivores in Waza National Park (Esser and Van Lavieren, 1979). These studies give a sense of what the floodplain was like prior to dam construction at the end of the 1970s.

After the construction of the dam, PhD and MA students from the Ecole de Faune (Cameroon), Dschang University (Cameroon), and Leiden University (Netherlands), conducted studies of the social and ecological systems in the floodplain and how they changed after the dam construction. Many of these students were supported by the Centre d'Étude de l'Environnement et du Développement au Cameroun (CEDC). Their research included studies of pastoralism (Schrader, 1986; de Bruijn, 1987; Moritz, 1994), fisheries (Van der Zee, 1987; Groeneveld, 1993; Harkes, 1993; van Est and Noorduyn, 1997), wildlife (Tchamba, 1996; Njiforti, 1997), vegetation (Oijen and Kemdo, 1986), and hydrology (Naah, 1990). Research on vegetation, wildlife, and pastoralism in the Waza-Logone floodplain has been synthesized in later papers (Scholte, 2007; Scholte et al., 2006; Moritz et al., 2019) and gives a good sense of both the short-term and long-term impacts of the dam on the social-ecological system of the floodplain.

A few months prior to opening the embankment, the Waza-Logone Project started a program to monitor the impact of the reflooding efforts, including hydrology studies of flood depth and duration (Sighomnou et al., 2002), wildlife populations (Scholte, 2013), migratory birds (Scholte, 2005), socio-economic studies of fisheries, and pastoralists (Scholte et al., 2006). A vegetation study was also conducted which examined changes in species composition along a transect that was monitored prior to the reflooding efforts (Scholte, 2007). These studies give a sense of the short-term impacts of the reflooding on the social-ecological system.

After the Waza-Logone Project ended in 2003, researchers continued to study the social-ecological systems in the floodplain, including the hydrology (Jung et al., 2011; Shastry et al., 2020; Murumkar et al., 2020; Vassolo et al., 2016; Westra and de Wulf, 2009; Delclaux et al., 2010), fisheries (Laborde et al., 2018, 2019; Laborde et al., 2016), and pastoralism (Moritz et al., 2019b, 2013). More recently, colleagues and students from the University of Maroua and the University of Ngaoundéré (both in Cameroon) as well as local non-profit organizations in Cameroon founded by former Waza-Logone project staff, have conducted studies of pastoral production systems (Mey et al., 2019), hydro-politics (Armel, 2016), fisheries (Ziébé, 2015; Mahamat and Diaouré, 2008; Labara et al., 2020), and resource conflicts (Khari, 2011). These studies give a sense of the long-term impacts of the reflooding on the social-ecological system.

Impacts of reflooding efforts

The short-term impacts of reflooding exceeded expectations: within five years perennial grasslands largely recovered, the numbers of waterbirds increased two-fold, the population of floodplain antelopes quickly increased, and livestock numbers doubled (Scholte, 2005). At the time, the Waza-Logone Project was considered a major success and showcased as an exemplary development project that restored both the ecosystem and supported the livelihoods of those living in the floodplain. Below we discuss the long-term impacts of the reflooding drawing from studies conducted in the last twenty years. We focus our analysis on the nexus of flooding, vegetation, wildlife, and pastoralism in the floodplain.

Flooding

The main driver of the coupled human and natural system of the Logone Floodplain is flooding. Floods are driven by rainfall in the larger basin of the Logone River, where rainfall has been decreasing since the 1960s (Murumkar et al., 2020). The seasonal patterns of flooding and flood recession drive vegetation and fish productivity, on which pastoralists, small-scale rice farmers, and fishers depend (Laborde et al., 2016). In the last four decades the changes in flooding patterns have resulted in two regime shifts (Moritz et al., 2016). First, the Maga Dam limited flooding and negatively impacted vegetation and fish biomass in the downstream floodplain (Scholte, 2005). The dam construction coincided with a period of below-average rainfall in the 1970s and 1980s, and a drought that further reduced seasonal flooding. The second regime shift happened when the Waza Logone project opened two waterways into the floodplain to partially mitigate the effects of the dam (Loth, 2004), which restored flooding to a much larger area. Around the same period, regional rainfall also recovered to average values (Delclaux et al., 2010), which further contributed to the restoration of the flooding regime. Finally, while climate change has led to a decrease in rainfall within the Logone watershed (Murumkar et al., 2020) and the growth in the number of fish canals has sped up the recession of the floodwaters (Laborde et al., 2016; Shastry et al., 2020), this has not yet resulted in another regime shift of flooding patterns.

Vegetation

To monitor how the floodplain vegetation would respond to the reflooding, researchers from the Waza-Logone Project focused on the three dominant perennial grasses: *Oryza longistaminata*, *Echinochloa pyramidali*s and *Hyparrhenia rufa*. The first year of reflooding the species showed a decline, which was followed by a relatively slow increase in the next four years (Scholte, 2005), but from the fifth year onwards, all three species showed a rapid and steady increase that seem to continue up to today, more than 30 years after the reflooding (Figure 4). Data from a grid in the park at the edge of the post-dam flood zone indicated that some perennial species (*Oryza longistaminata*, *Echinochloa pyramidalis*, *Vetiveria nigritana*) only re-appeared two decades after the reflooding, suggesting that some of the ecological processes are happening much slower, requiring long-term observations. The vegetation studies indicate that the reflooding impacts on vegetation are enduring, that flooding is the main driver of this coupled system, and that long-term monitoring is critical for assessing the impact of reflooding.

Wildlife

Wildlife surveys conducted in the last five decades show that the populations of kob (*Kobus kob*) and korrigum (*Damaliscus lunatus korrigum*) decreased significantly after the construction of the dam and showed only a marginal increase after the reflooding efforts (Scholte et al., 2007, 2013) (see Figure 5). In the last fifteen years, the numbers of these herbivores have decreased considerably. Other wildlife species, like lions (*Panthera leo*) have also diminished in numbers (Tumenta et al., 2010). A combination of interrelated reasons may explain the reduction in wildlife numbers in Waza National Park, including shrinking operating budgets of the park, fewer guards, and increasing insecurity in the region. This insecurity included the kidnapping of a family of tourists, leading to tourism collapse and decreasing tourism revenues (Scholte, 2020). Thus, despite the reflooding efforts, which improved habitat for herbivores, wildlife populations have continued to decline.

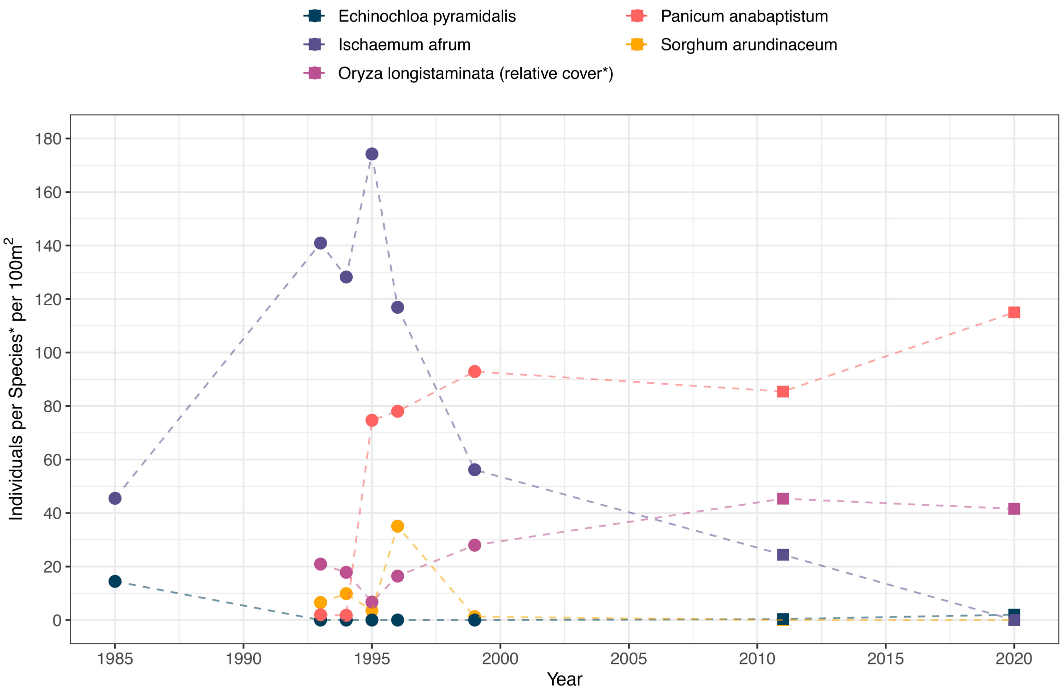

FIGURE 4
Changes in vegetation in Waza National Park, 1985 – 2020. Data from longitudinal study of 23 10-by-10-meter plots within a 1 x 0.5 km area in Waza National Park at the edge of the floodplain (Scholte, 2005:95) with preliminary results from 2011 and 2020 (Scholte, in preparation).

Pastoralism

The Logone Floodplain has long been a very important dry season grazing area for pastoralists in the Chad Basin, including pastoralists from neighboring Niger and Nigeria (Beauvilain, 1981). Access to the grazing areas is open for all pastoralists regardless of nationality, ethnicity, or seniority (Moritz et al., 2013) and studies show that pastoralists in the floodplain have always adapted to changing ecological and political conditions that affect grazing and safety (Moritz et al., 2019; Schrader, 1986; Scholte et al., 2006). A census of pastoralists in the floodplain that started just before the reflooding and continued for five years after reflooding showed that pastoralists quickly adapted to the improved grazing lands by either staying longer in them or returning to the floodplain after having moved elsewhere because of the desiccation of the floodplain (Scholte et al., 2006). This resulted in a three-fold increase in grazing intensity that stabilized from 1997 onwards with no signs of overgrazing. A long-term study of pastoral mobility and grazing pressure showed evidence that mobile pastoralists distribute themselves in an ideal free distribution in which the distribution of grazing pressure matched that of the grazing resources (Moritz et al., 2014a, 2014), even after the arrival of thousands of pastoralist refugees from Northeast Nigeria following the rise of Boko Haram (Moritz et al., 2019). This evidences that pastoralists use of common-pool grazing resources functions as a self-organizing complex adaptive system that is resilient, equitable, and sustainable (Moritz et al., 2018).

One of the goals of the reflooding efforts was to reduce competition between livestock and wildlife in Waza National Park (Scholte et al., 2006). The assumption was that the reflooded areas outside the park would offer enough grazing for their livestock and would stop pastoralists from grazing their animals in the park. While these efforts were initially successful (Scholte et al., 1996), pastoralists later used the park not in search of forage but to seek refuge from insecurity in the floodplain (Scholte et al., 2022a) (Figure 6).

Insecurity

The greater Chad Basin has a long history of insecurity, and this has affected the inhabitants of the floodplain directly and indirectly for centuries (Beauvilain, 1989; Mohammadou, 1983). In the decades that we have worked in the floodplain, insecurity was a major concern for floodplain inhabitants as it threatened their lives and livelihoods. This insecurity took different forms, including clashes between Arab pastoralists and Kotoko fishers, amplified by national party politics; low-level insecurity in the form of cattle thefts and raids that frequently resulted in loss of life; armed banditry that involved hold ups, car jackings, and kidnappings; terrorist attacks by Boko Haram; and the violence committed by agents of the state. These insecurity problems were also present when the Waza Logone Project was active in the region. Because the insecurity affected populations in the floodplain alongside project personnel, the project leadership advocated for greater engagement of the government in the security problems (Scholte et al., 1996). While greater government engagement improved security in the floodplain, it came with excessive force, torture, and extra-judicial killings by security forces (Moritz and Scholte, 2011). In the decades since reflooding, insecurity

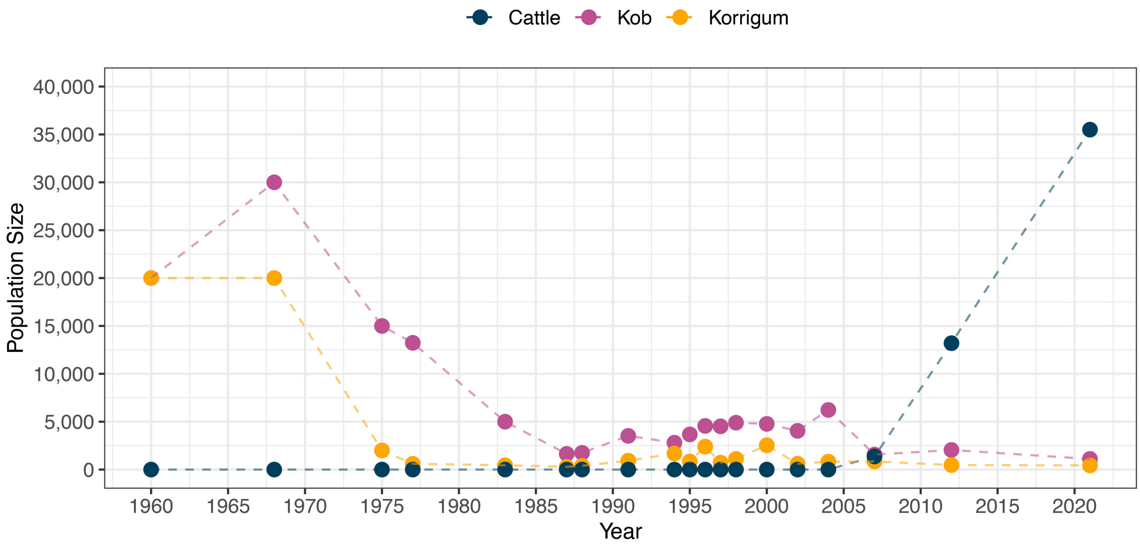

FIGURE 5
Numbers of kob, korrigum, and cattle in Waza National Park, 1960-2021. Dam construction in 1979 resulted in a decline of kob and korrigum numbers, reflooding in 1994 and 1997 resulted in a short-term increases in antelope numbers, and insecurity in the floodplain resulted in a major increase in the number of cattle seeking refuge in the park in 2019 (updated from Scholte (2013) and Scholte et al. (2022a).

continues to be a major concern in the Logone Floodplain and neighboring Waza National Park. In particular, the terrorist attacks and threat of Boko Haram (Kelly Pennaz et al., 2018; Moritz et al., 2019) alongside the more recent widespread communal violence between Arab pastoralists and Musgum fishers (Scholte et al., 2022a) continue to pose major security challenges. Insecurity increased pressure on the park and its wildlife as pastoralists sought safety near or in the park (Scholte et al., 2022a, 2022b).

Discussion

In many ways, the reflooding efforts of the Waza-Logone Project were a success. It led to a steady recovery of vegetation, fish populations, and livestock numbers that continues through today. Long-term monitoring of different systems shows different outcomes: vegetation and pastoralists continue to benefit from reflooding, but wildlife in and outside Waza National Park have not.

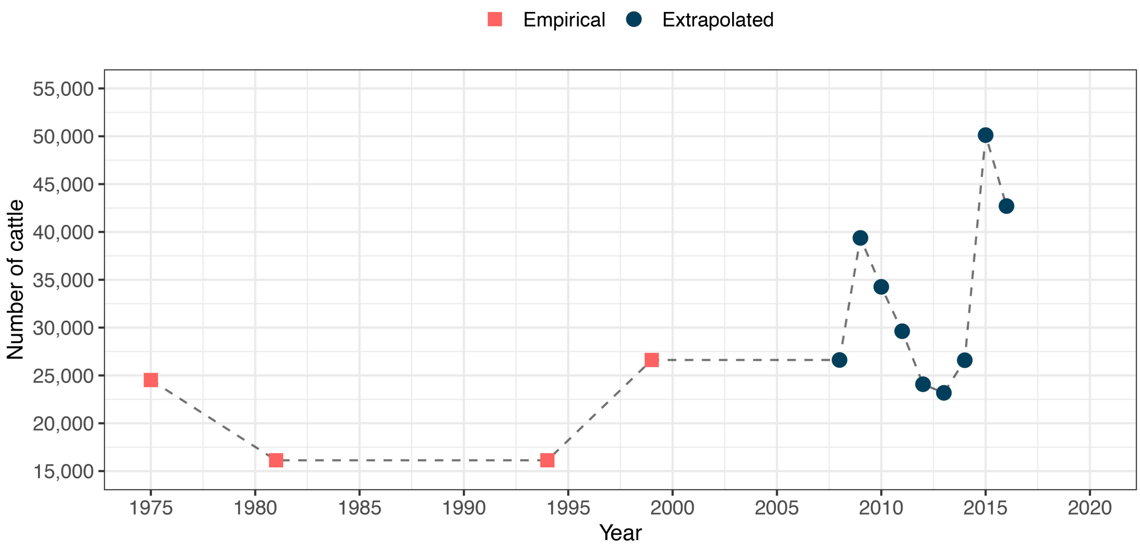

FIGURE 6
Number of cattle in the central floodplain, 1975-2016. The figure shows the trends in the number of cattle in the central floodplain, directly east from Waza National Park. The data marked in red are from empirical studies of cattle numbers and the data marked in black have been extrapolated from several studies of pastoralism in Logone Floodplain reviewed in Moritz et al. (2019:40). The high number of cattle in 2015 and 2016 is due to the arrival of pastoralists fleeing the terror of Boko Haram in neighboring Northeast Nigeria.

Assessing the impacts of reflooding and the state of the coupled human and natural systems of the floodplain yields different results depending on the time period. Five to ten years after reflooding, it was considered a great success, but now, 25 years later, not so much. Wildlife suffered from insecurity and lack of investment in the park. The Waza-Logone Project was working on the assumption that the government would continue to invest in Waza National Park and support the protection of wildlife. While flooding is the main driver of the social-ecological system, a long-term perspective shows how important the larger economic and political context is. Rewilding or reflooding does not happen in a vacuum; insecurity had a major impact on human and wildlife populations.

The Waza-Logone Project had a vision of the floodplain as a social-ecological system, but that vision also had its blind spots. In particular, farming was not part of that vision, most likely because it was less compatible with wildlife conservation and other forms of land use like pastoralism and fisheries. No monitoring studies focused on farming in the floodplain – the focus was on fisheries and pastoralism – even though Musgum fishers in the floodplain were also engaged in rice farming. After the reflooding, there has been a steady expansion of dry season sorghum cultivation at the periphery of the floodplain and later large-scale rice cultivation right in the middle of the floodplain. The goal of the Waza-Logone Project was that the social-ecological system would be restored with the reflooding. The implicit assumption was that communities would continue to make a living as they were doing at that time with fishing, herding, and some farming. A co-management approach to the Waza-Logone project and following the reflooding, to the park, could be beneficial in rewilding as it better accounts for the livelihood concerns of communities who use the area, while engaging them in conservation goals and processes.

The Waza-Logone Project was active for less than ten years in the floodplain. The project was informed by studies conducted in the past. Expatriate and national experts worked on the project for only a few years. They could not imagine how the floodplain would change and how communities would continue to shape the anthropogenic landscape. However, communities in the floodplain have always changed and adapted and continued to do so in response to the construction of the dam and the reflooding efforts. In the last two decades, communities innovated and adapted in response to flood restoration, e.g., by digging more and longer fish canals, digging artificial ponds to capture more fish, practicing aquaculture in the rivers, and clearing larger rice fields and more sorghum fields – all different ways to make the floodplain more productive for humans and which demonstrate their already vested interests in ecosystem management. In hindsight, it would have been better to develop alternative scenarios for how the floodplain could develop, including how political, economic, and demographic changes may affect the social-ecological system of the floodplain.

Conclusion

All natural systems are affected by human systems and vice versa, which means that the framework of coupled human and natural systems is useful to study and manage systems that are considered "more natural" like parks and wilderness, as well as systems that are "more human" like cities and agricultural areas. The Waza-Logone Floodplain has both – Waza National Park and the Logone Floodplain. Conserving wildlife in the park was one of the motivations for the reflooding effort, but not the only one. The reflooding effort of the Waza Logone Project was a landscape-level intervention that considered how Waza National Park is embedded in the larger Logone Floodplain.

The reflooding effort did not restore the social-ecological system as before the dam, but key hydrological and ecological processes were restored. However, our review shows that while human populations in the floodplain have benefitted from the reflooding, wildlife populations in Waza National Park and the floodplain have declined, despite the reflooding and the recovery of floodplain vegetation. Restoring the hydrological and ecological processes was necessary but not sufficient for supporting wildlife; political dynamics impact the ecological processes and have to be considered for rewilding to succeed.

African floodplains, like the Logone Floodplain, are tightly coupled human and natural systems that are of great importance for humans and wildlife. These floodplains have always been anthropogenic landscapes, shaped by humans in one way or another, to make it more productive for them. Supporting or restoring the natural flooding patterns is critical for maintaining the productivity of floodplains for humans and wildlife, but in the Logone Floodplain humans have been able to more successfully adapt to the reflooding than wildlife in Waza National Park.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Ethics statement

The paper is based on a review of published and unpublished studies of the Waza Logone Floodplain.

Author contributions

MM: Conceptualization, Writing – original draft, Writing – review & editing, Visualization. CH: Conceptualization, Writing – original draft, Writing – review & editing, Visualization. PS: Conceptualization, Writing – original draft, Writing – review & editing

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Building alliances and consensus around social-ecological rewilding in Chile

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We provide a case study of how we position our rewilding project in central Chile in order to find scientific and social support and build alliances, collaborations, and consensus. Our core vision focuses on reintroducing guanacos (*Lama guanicoe*) to central Chile in order to provide natural restoration and ecosystem processes in *espinal* woodlands dominated by the native tree *Vachellia [Acacia] caven*. We envision a scenario of "social-ecological rewilding" with widespread guanaco browsing in woodlands and guanaco migration across the region, coexisting with multiple human uses of the landscape. Guanacos would ideally be managed by regional collectives who could benefit from guanaco tourism, sustainable harvest of their fiber (wool), and regulated hunting. Our wider vision for reintroductions and integrated conservation management extends to a set of other species that may have coexisted with guanacos and *V. caven* at various points in the past, but more research is necessary to establish and gain support for evidence-based baselines. Our strategy is to inspire actors with greater resources (land, money, influence) to share our vision and implement it, in collaboration with the NGO that we have formed to support our projects. Over ten years, circulating alternate interpretations and a novel imaginary of how central Chile was in the past and could be in the future, along with developing and testing scientific hypotheses, has moved our vision from an idea shared by two people to one that a wide variety of actors publicly embrace.

KEYWORDS
guanaco (*Lama guanicoe*), rewilding, Chile, *Vachellia caven*, social-ecological system

Introduction

Rewilding is a conservation movement that has multiple origins (e.g. Soulé and Noss, 1998), some of which crystalized as frustrations with traditional conservation and its focus on short-term population and species targets (Jepson, 2022). It is expanding and becoming a legitimate option for management within some parts of Europe (Carver et al., 2021; Segar et al., 2022), although it is not immune from social conflicts (Wynne-Jones et al., 2018; Pellis, 2019). There are emerging projects and opportunities around the world, including in South America (Root-Bernstein et al., 2017a). As we understand rewilding, it conducts species reintroductions for restoration, that is, targeting keystone and ecosystem engineering species in order to restore missing ecosystem functions and processes. This functionalist aim leaves room to consider the use of proxy taxa with similar ecological functions to extinct species (Griffiths et al., 2010). In addition, we think of rewilding as favoring a redistribution of agency, autonomy and regulation from humans back towards other species, commonly referred to as "passive management". There can thus be different degrees of rewilding (Pedersen et al., 2020). This, in turn, implies accepting the possibility of changing, unknown, and non-analogue ecological states and trajectories (Williams and Jackson, 2007). We support a coexistence position, in which restoration of ecosystem processes and passive management are compatible with human interactions with nature (Carver et al., 2021; Guerrero-Gatica et al., 2023).

In this paper we describe our vision for rewilding in central Chile, a project which we envisioned beginning ten years ago in 2014. We describe our strategies for building alliances and consensus around the project, and how this allows us to overcome barriers such as lack of data, capacity, funding, control over land, or political influence. Some questions for further research, to which we do not yet have answers, can be found in Appendix 1 (Supplementary Material).

Context

Central Chile, understood as including the administrative regions from Maule to Coquimbo, is a mediterranean-climate region of significant plant endemicity and global conservation priority (Myers et al., 2000; Scherson et al., 2014). Its main habitat types are espinal early-successional open woodland, matorral shrubland and sclerophyllous forest, forming mosaics according to hillslope aspect, disturbance history, and other factors. These habitats are linked by succession (Root-Bernstein et al., 2017b). Espinal is used as a silvopastoral woodland, and is dominated by *Vachellia [Acacia] caven*. The majority of woodlands and forests in central Chile are spontaneously recovering from historical clearing for charcoal production or agriculture (Schulz et al., 2010; Vergara et al., 2013; Root-Bernstein et al., 2017b). Chile is characterized by a terrestrial mammal fauna dominated by species < 100 g, likely due to biogeographic isolation and Pleistocene-Holocene megafaunal extinctions (Mella et al., 2002; Hernández-Mazariegos et al., 2023). Extant camelids and deer are extirpated from most of central Chile, although these have been ecologically replaced to some degree by free-range cattle, horses, and sheep. A greater richness of medium and large animals was present in central Chile prior to the megafaunal extinctions in the late Pleistocene/early Holocene, followed by a wave of extirpations after Spanish colonization (Root-Bernstein et al. in submission; Carrasco, 2002).

Central Chile has long been regarded as degraded, in ways that are intertwined with the history of land reform, rural development and a neoliberal economic approach (Armesto et al., 2010; Solimano, 2009; Root-Bernstein, 2014). It is undervalued as "Nature", densely populated, and extensively converted to industrial agriculture (Romero et al., 2003; Schulz et al., 2010; Root-Bernstein, 2014). In 2002 less than 2% of the central zone was under state protection (Pauchard and Villarroel, 2002) and in 2011 94% of central zone vegetation types had less than 10% of their area under state protection (Pliscoff and Fuentes-Castillo, 2011). In 2022, the situation had improved with 3.99% of the central zone (Coquimbo-Maule) under state protection (calculation based on Pliscoff, 2022) and only one vegetation type lacking any kind of protection ("thorny mediterranean forest of *V. caven* and *Lithraea caustica*") (Pliscoff, 2022). According to Petit et al. (2018), only two public protected areas in central Chile have effective management plans. This protected area gap is partly compensated for by private protected areas (Schutz, 2018; Pliscoff, 2022), but these lack strong legal protections (Root-Bernstein et al., 2013). Apart from the translocation of injured or problem animals, there has to our knowledge only been a very small number of translocation or reintroduction projects in Chile, focusing on huemul (*Hippocamelus bisculsus*) and guanacos (Vidal et al., 2018), some of which are not publically documented. Restoration work focuses on the elimination of invasive species and tree planting (Medina-Vogel et al., 2015; León-Lobos et al., 2020). To the best of our knowledge, there is only one other initiative that identifies itself as rewilding in Chile: the reintroduction of Darwin's rhea (*Rhea pennata*) in Pumalín Douglas Tompkins National Park and Patagonia National Park, until 2019 a Nature Sanctuary owned by Pumalín Foundation. This project is carried out by the foundation Rewilding Chile, until 2021 known as Tompkins Conservation Chile, which along with the Pumalín Foundation is the Chilean branch of the Conservation Land Trust based in California and funded by the businessman Douglas Tompkins.

Ownership of non-agricultural land in Chile is dominated by private landholdings called *fundos*. These are the remnants of the latifundia system put in place by the Spanish colonists, in which colonial landowners benefited from the labor of peasants, many of whom were essentially serfs (*inquilinos*) often kept in debt to the landowner and paid in kind rather than in money. Other mestizo peasants roamed central Chile as itinerant jack-of-all trade workers (*gañanes*). The social order changed with the Land Reform that took place in the period between 1962-1973, in which many *fundos* were expropriated by the state and transferred to peasant collectives (Wright, 1982; Kurtz, 2001; Murray, 2003). This process was arrested and to a large extent reversed following the coup in 1973, and many landholdings were sold to third parties who then invested in industrial agriculture, including pine and eucalyptus plantations, vineyards and fruit orchards (Kurtz, 2001; Murray, 2002). Since then, industrial agriculture for export has been the focus of investment in rural development. On the positive side many former *inquilinos* and other peasants ended up as smallholders owning or renting their land, with diversified livelihoods animated by a variety of non-monetary values (Root-Bernstein, 2020; Root-Bernstein et al., 2020). However, these values are viewed as antithetical to rural development, and a transition to micro-enterprises and market-oriented production is favored by PRODESAL, the government office supporting smallholders (for a comparable situation in the south of Chile, Di Giminiani, 2018). This stance is shared by environmentalists, who see cattle raising and other traditional management and resource-use practices as antithetical to conservation— the elimination of peasant livelihoods was described as a policy of CONAF, the government Forestry department, as part of their strategy to meet Convention on Biological Diversity and climate change targets (pers. comm. C. Ravanal to MR-B 2019). A widespread discourse directed at *ganaderos* and *arrieros*, two traditional livelihoods focused around non-intensive cattle and horse raising, urges them to give up their way of life and invest their money in ways that will allow them to aspire to the middle class (compare Mayol Miranda et al., 2013).

Although central Chile does not have rural practices recognizably rooted in an indigenous background and is not a legally recognized indigenous area, it is a region with strong mestizo peasant traditions and identity. In rural areas and small towns, many people mix wage labor, for example working for national and local government administration or for the mining industry, with diversified smallerholder subsistence farming (Root-Bernstein et al., 2020; Guerrero-Gatica et al., 2023). Traditional cattle raising in espinal, and later-successional woodlands still occurs but is increasingly under pressure as *fundo* landowners reneg on traditional rights of access. Although there is a positive trend in the increase of private landholders setting aside their land for conservation (Schutz, 2018), it is concerning to us that the majority consider appropriately pro-environmental management to be anti-cattle and anti-resource use, in the absence of any local empirical studies to back up this conclusion. In central Chile, cattle are typically kept not for market-oriented production, at low densities with little human contact, practically in the same way as rewilded cattle in Europe, as a traditional practice with symbolic cultural importance. Other traditional timber and non-timber forest resources include charcoal production from *Vachellia [Acacia] caven*, production of *tierra de hoja* (a kind of natural compost) from leaf raking (leaf litter collection) in woodlands dominated by *Peumus boldus* and *Lithraea caustica*, collection of the bark of *Quillaja saponaria* for soap production, collection of *Peumus boldus* leaves and other medicinal herbs such as *Haplopappus* spp. for herbal tea, and collection of the mini coconuts of the endemic Chilean palm *Jubaea chilensis* (Caucheteux unpublished data; see also Moyano Altamirano, 2014). Small-scale honey production in sclerophyllous forest has been introduced as a successful export product. The ecological impacts of all of these activities (except honey production) are assumed to be negative but have not been studied. We hypothesize that, in the absence of any large native browsers or soil disturbers, the reduction of cattle and horse grazing by exclusion, and the reduction via regulation of leaf raking, may together contribute to increasing the intensity of wild fires, which is a serious and increasing problem in central Chile (Urrutia-Jalabert et al., 2018; compare Mathews and Malfatti, 2024).

History of the project

The origin of our vision of social-ecological rewilding in central Chile was learning that the espino *Vachellia [Acacia] caven* in silvopastoral espinal woodlands can be managed by pruning and coppicing, in order to produce compensatory growth, and a cascade of benefits (A. Olivares pers. comm. 2013; Olivares, 2016). We hypothesized that the extant animal most likely to be a potential co-evolutionary partner and browser of trees is the guanaco (*Lama guanicoe*), as we explain in the next section (*Justification*). The first phase of the project (2014-2016) was a naturalistic experiment with five guanacos, to understand if they do browse *V. caven* and how this tree responds (Root-Bernstein et al., 2016; Root-Bernstein et al., 2024a). The result was that guanacos spontaneously browse *V. caven*, which shows compensatory growth, as predicted.

The second phase of the project (2017) was the release of the experimental guanacos in the private Cascada de las Ánimas Nature Sanctuary (Guerrero-Gatica and Root-Bernstein, 2019; Figure 1). The result was a gain in knowledge and experience with the regulations and practicalities of native animal translocation, for which there is little institutional experience in Chile. The third and ongoing phase of the project (2019-present) is the creation of a guanaco rehabilitation and breeding center in the same nature sanctuary. The fourth phase, for which our partners are currently seeking funding, was envisioned in 2021 when we were contacted by Sara Larraín, an environmental philosopher and political activist with her own environmental NGO (Chile Sustentable), to co-develop a project to reintroduce guanacos into the San Francisco de Lagunillas y Quillayal Nature Sanctuary (Figure 1). Subsequently the proposal evolved into a much larger project that intends to create a corridor of private landholdings and public protected areas in the Andes to the east of the capital, Santiago. Sara Larraín, in collaboration with the guanaco expert Benito González, has developed a plan that will incorporate both passive repopulation of guanacos from Argentina across the corridor and our planned active release program in Cascada de las Ánimas (phase three).

Three events were also important in bringing together a community of collaborators and supporters. The first was a symposium on guanaco rewilding that we organized with the Center for Applied Ecology and Sustainability, Pontificia Universidad Católica de Chile, in 2019, to which we invited a large number of Chilean guanaco experts and NGOs, including WCS Chile. This led to a second important event, which was the invitation to take part in a working group led by WCS Chile on guanaco conservation in central Chile. The report from the working group was presented at an event in May 2024 (Silva et al., 2024). This event brought together an even broader set of associations and interested parties. Actors who support our work and share our broad vision include several private landowners, certain private protected areas, some public protected area officials, other environmental NGOs active in Chile, academic researchers, individuals from the arts and traditional crafts sectors, in addition to students, volunteers and other members of the public who engage with our NGO through our outreach activities. The third

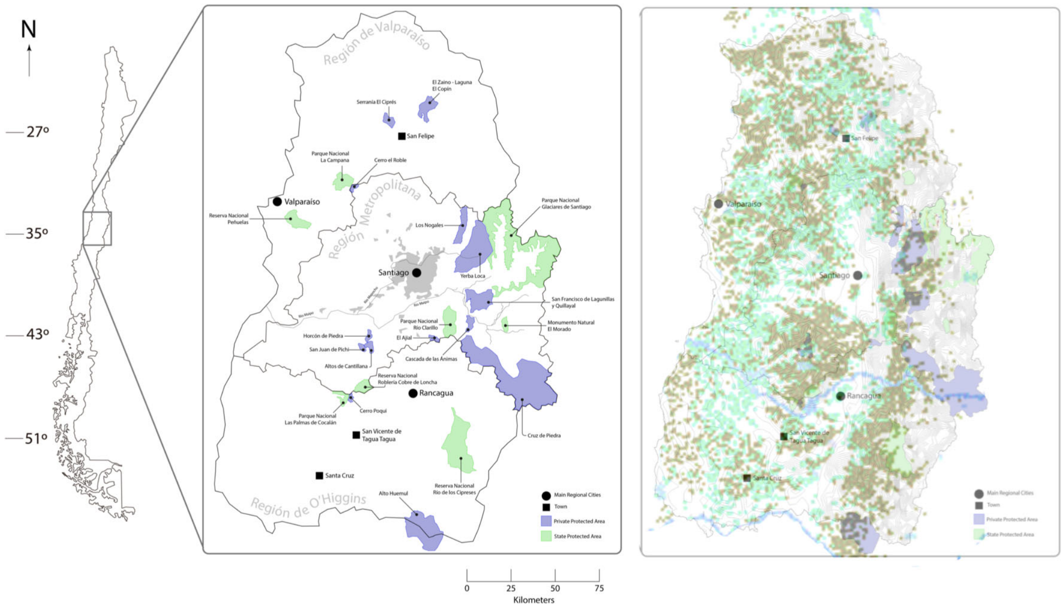

FIGURE 1
Map showing public and private protected areas in three regions of central Chile. This includes areas where we currently work, and areas where hope to work in the future. Inclusion on this map does not indicate current collaboration with our project. In the map on the left, in purple, private protected areas and nature sanctuaries; in green, public reserves and national parks; in light gray, the urban area of Santiago. On the right, grey lines indicate altitude isoclines, light green dots indicate espinal habitat and olive green dots indicate sclerophyllous forest. Land cover is adapted from Root-Bernstein and Svenning (2017) as allowed by the license.

important event was that, in 2023 and after 3 years of effort, we formed ourselves as a legal NGO, Kintu.

Justification of the project

Ecological restoration justification

We see rewilding as contributing to a restoration of central Chile, although rewilding and restoration are different concepts (Corlett, 2016; Derham, 2019; du Toit and Pettorelli, 2019). Our initial hypothesis, that guanacos are the browsing species to which *V. caven* compensatory growth is an adaptation, draws on a corpus of work on the ecological and silvopastoral benefits of coppicing and pruning espino (Benedetti, 2012; Olivares, 2016). This work shows that coppicing and pruning results in compensatory growth and increase in the tree canopy area, which can lead to a positive cascade of effects increasing ecological and agricultural productivity (Olivares, 2016). This corpus of work was thus the justification for our initial experimental phase of the project. Browsing large herbivores have been absent from almost the entire range of *V. caven* in central Chile for around 500 years, so there was no scientific knowledge on this interaction. Our results show a nuanced outcome (Root-Bernstein et al., 2024a). The resulting net compensatory growth was relatively small. The implications for how best to use guanacos as a restoration tool remain to be developed. Our resulting hypotheses are that *V. caven* may be adapted to more intense or damaging browsing than what is provided by guanacos, and that this may have been historically provided by the large number of megaherbivores present in the range of espino through the early Holocene (Root-Bernstein et al., 2024a). We also noticed that guanacos have potential non-trophic ecological impacts such as facilitation of plant growth around dung middens (Guerrero-Gatica and Root-Bernstein, 2019). We are currently carrying out experimental research to document these impacts and to assess whether they are beneficial or harmful to the ecosystem on balance.

Historical baseline justification

The historical pre-Columbian ranges of both guanacos and *V. caven* are well-established (e.g. IUCN), making them native to Chile and with overlapping historical ranges. Initially we took this as sufficient justification to study the potential ecological impacts of reintroducing guanacos into central Chilean habitats with *V. caven*. Historical baselines in restoration are, today, often understood as providing data to inform the management of future non-identical ecosystems (Gillson and Marchant, 2014; Beller et al., 2020). In line with this position, we are actively researching the development of historical baselines that can inform the management of future ecosystems in central Chile (Root-Bernstein et al. in submission). These baselines may or may not support our current vision, but we will adjust our vision in an evidence-based manner. Additionally, stakeholders sometimes raise questions about nativeness and naturalness of these species and their interaction. Proving that guanacos and *V. caven* are native to Chile (e.g. with earliest dates of presence in the Chilean parts of their ranges compared to dates of speciation) and that the interaction is natural (i.e. the two species have a significant coevolutionary history) raises a number of evidentiary challenges. We discuss how we deal with this issue below.

Guanaco population conservation baseline

One of the criteria for a successful reintroduction project can be the stabilization of a viable population (Robert et al., 2015). It was not our original goal to reintroduce guanacos in order to contribute to creating a viable population. Guanacos are not globally considered endangered (Baldi et al., 2016) although they are considered vulnerable in central Chile, due to their historical extirpation (especies.mma.gob.cl, visited 18/7/2024). Currently, guanaco population dynamics specialists are pursuing a strategy of allowing passive repopulation of areas from which guanacos have been historically extirpated (pers. comm. B. González 2024). Our proposal that guanacos could be actively reintroduced on the basis of other justifications described here, puts us in apparent conflict with this position (although stage four of our project envisions both active and passive reintroduction). We discuss below how we engage with this potential conflict.

Cultural values justification

Some scholars claim that values emerge from collective experiences of emotion and transcendence (Durkheim, 1912; Dewey, 1939; Joas, 2023). Other theorizations argue that value emerges from symbolic exchanges and transformations (Mauss, 1950; Appadurai, 1988; Graeber, 2001). The French tradition of environmental ethics provides another perspective (Larrère, 2006). Once established within a culture, values are mobilized in multiple contexts and according to multiple evaluative frames and registers, which are subject to conflict and negotiation (Maris et al., 2016; Heinich, 2017). Conservationists expect a set of environmental values to motivate pro-environmental actions (Chan et al., 2016; Tadaki et al., 2017; Chan, 2020; IPBES, 2022). Because rewilding may ultimately have socially transformative impacts (IUCN Rewilding Thematic Group, 2018), the emergence of new collective values could be a result of the project. In the first instance, however, we focus on understanding how existing values are mobilized to justify and motivate actions in the central Chilean context.

Research we carried out before this project started pointed to the low public valuation of and tenuous attachments to central Chilean landscapes (Root-Bernstein, 2014), related to their perception as being underdeveloped, degraded and associated with poverty (Beau, 2017). We identified central Chilean species that were widely recognized, although not universally loved—including *V. caven* (Root-Bernstein and Armesto, 2013). Before phase one of the project was implemented, we carried out a questionnaire-based study to assess the values that Chileans would refer to, to support or oppose a hypothetical guanaco reintroduction project in central Chile (Lindon and Root-Bernstein, 2015). When we presented the guanaco as native to the region (which many people are not aware of), support for the hypothetical project was high. The values referred to included the intrinsic value of nature and our moral obligations to protect it, the increased aesthetic value of seeing guanacos in central Chilean landscapes, the value of the guanaco as a cultural symbol of South American or Chilean wilderness, and potential economic benefits (Lindon and Root-Bernstein, 2015). We found comparable results when we repeated the study in the rural community where the third phase of the project is underway (Guerrero-Gatica et al., 2023). This aspect of the research is not complete, and the project requires a constant dialogue around cultural values, justifications and acceptability with potentially affected populations, through a co-construction approach (Guerrero-Gatica et al., 2023).

Economic benefits justification

As we found in our original study on public support for guanaco reintroduction in central Chile (Lindon and Root-Bernstein, 2015), economic benefits may garner support for the project. The neoliberal pro-entrepreneurship context also supports developing this justification (Kurtz, 2001; Murray, 2002; Di Giminiani, 2018). Guanaco observation, as a form of nature tourism, is one proposition that could attract investment and also be a source of income for rural people who already have relevant knowledge and skills (Guerrero-Gatica et al., 2023; pers. comm. Adrián Tapia 2024). Guanaco fiber, sheared sustainably and with high animal welfare (Carmanchahi et al., 2022), is currently commercialized as luxury textiles in Peru and Argentina. Perhaps this industry could also be established in Chile.

Vision and hopes for the future of the project

Our rewilding vision can be expressed in the form of several propositions that orient our scientific research and applied work. These propositions are similar to hypotheses but are not stated with scientific rigor; rather multiple scientific hypothesis can be derived from them. They are also not goals, although goals can also be derived from them. By propositions we mean assertions, with supporting arguments, about the true or the possible:

- *Reintroducing guanacos to espinal will restore beneficial ecological cascades.*
- *Guanacos belong in central Chilean woodland mosaics.*
- *The espino* Vachellia [Acacia] caven *is a beneficial native tree that should be protected in central Chile.*
- *Involvement of local communities is essential.*
- *Multi-species rewilding can be scaled up across all of central Chile.*

Reintroducing guanacos to espinal will restore beneficial ecological cascades

Our results (Root-Bernstein et al., 2024a) suggest that guanacos can play a role in stimulating the established beneficial ecological cascades increasing productivity as a result of compensatory growth in espinal (Olivares, 2016). We speculate, but have at this point no experimental evidence for central Chile, that guanacos could contribute to ecosystem functions and processes such as fire control (by eating the herbaceous layer; Rouet-Leduc et al., 2021), soil nutrient cycling (via dung middens; Veldhuis et al., 2018), shade and soil moisture provision (through their impacts on *V. caven* canopies; Olivares, 2016), and landscape level connectivity (seed and nutrient dispersal during seasonal migration; Bauer and Hoye, 2014). It is important to note that our vision is flexible and can adapt to evidence as it is produced. For example, our experiment in phase one suggested that guanaco browsing, even at high densities, has a smaller positive effect than optimized coppicing and/or pruning (Root-Bernstein et al., 2024a). This turned our attention to other (extinct) species to which espino compensatory growth may be adapted, thus expanding our vision to other rare, missing or potentially missing species (see below).

Guanacos belong in central Chilean woodland mosaics

The guanaco is strongly associated with Patagonia and Tierra del Fuego, where it is abundant, and is a Chilean symbol of wilderness (Lindon and Root-Bernstein, 2015). However, as noted above, guanacos are recognized as previously having a native range across the entire Southern Cone of South America (Gonzalez et al., 2006). Guanacos are generalist grazers and browsers that live in a wide range of habitats. Guanacos are currently found in semi-arid wooded habitats including open woodlands of Argentina, and the Chaco in Bolivia (Gonzalez et al., 2006; Cuéllar Soto et al., 2017). Researchers of remnant guanaco populations in the Argentinian Chaco consider that guanacos lived there both before and during at least 3000 years of human occupation (Costa and Barri, 2018). However, guanacos living in wooded areas is regarded by some researchers in Chile as unnatural, an outcome of avoiding anthropogenic pressure (e.g. Puig et al., 1997; Cavieres and Fajardo, 2005; Muñoz and Simonetti, 2013).

It is difficult to obtain evidence of paleoecological or historical species interactions between a tree and a large herbivore. Microwear evidence from fossil guanaco teeth would reveal whether guanacos in central Chile were mixed grazers and browsers as they are across their range (e.g. Rivals et al., 2013), but such evidence would not indicate precisely which species was being browsed. Like other acacia pollens, *Vachellia (Acacia) caven* pollen does not register in lake sediments. A positive functional adaptive interaction would also not in itself be evidence of co-evolution (Root-Bernstein et al., 2024a). Historical records that we are aware of do not describe precisely what guanacos in central Chile ate. We thus do not expect to ever have definitive proof that guanacos browsed on *V. caven* in central Chile at specific times in the past. From a scientific perspective, we are content with a functionalist rather than a compositionalist justification for their reintroduction (Gillson et al., 2011).

In addition, government policy is that guanacos from Patagonia and Tierra del Fuego, where the population is abundant and subject to lethal control to reduce its numbers, cannot be released in central Chile (pers. comm. Servicio Agrícola y Ganadera 2017, pers. comm. Servicio Agrícola y Ganadero, 2023). Particularly, the Servicio Agrícola y Ganadero cited the “genetic issue” as an important barrier to reintroducing guanacos from Tierra del Fuego, which at the same time is the only place where the state allows removal of guanaco individuals, due to the good status of the population (pers. comm. Servicio Agrícola y Ganadero, 2023). The “genetic issue” is related to whether it is safe to interbreed different guanaco populations. Genetic studies have shown that the Patagonian and Tierra del Fuego populations are all descended from northern populations in the last several thousand years (Hernández et al., 2019) although recent habitat fragmentation is leading to differentiation between the populations (Sarno et al., 2015; León et al., 2024). León et al. (2024) claim that there are two subspecies of guanacos, one in Peru and one in the rest of South America, in contrast to earlier papers that found inadequate differentiation to substantiate the existence of any subspecies (Gonzalez et al., 2006; Marín et al., 2008). León et al. (2024) also express the opinion that reintroductions and translocations of guanacos should be carried out with extreme conservatism, given that they identify a handful of genes for certain enzymes that differ between populations within the southern subspecies. In contrast, Frankham and colleagues recommend assessing the risk of outbreeding depression from crossing distantly related populations and the risk of inbreeding depression from not re-connecting fragmented populations (Frankham et al., 2011).

To obtain legally releasable guanacos in the short term, we have partnered with the Cascada de las Ánimas Nature Sanctuary to develop phase 3 of our project. The center will be able to accept guanacos from the region that are injured and cannot be re-released into the wild. However, we will legally be allowed to release their offspring into the wild because they are from a local population. We hope that the first release of guanacos bred in the rehabilitation center can take place within 5-10 years.

The espino *Vachellia [Acacia] caven* is a beneficial native tree that should be protected in central Chile

The tree *Vachellia [Acacia] caven* (locally called *espino*), the megafloral partner in this project origin story, has an almost opposite public perception to guanacos, as it is associated both in the popular imagination and in scientific research, with poverty, degradation, and poor land management by peasants (Root-Bernstein, 2014). Early ecological research in central Chile proposed a pre-colonial ecological baseline of a primary, closed, continuous sclerophyllous forest (Armesto and Gutierrez, 1978; Solbrig et al., 1977). By the 1990s, a time which not coincidentally was a peak of smallholder agricultural clearing and charcoal production and thus of anthropogenic disturbance across rural landscapes, a consensus had emerged that espinal was a degradation of sclerophyllous forest (e.g. Aronson et al., 1993; Ovalle et al., 1999; van de Wouw et al., 2011). The scientific literature from this period often states that *V. caven* is invasive, without clearly distinguishing between invasive in the sense of non-native and invasive in the sense of entering and degrading other habitat types through rapid growth and competition. Effectively, *V.*

caven also occurs in the Chaco, from where it is presumed to originate (although there is no evidence as to where the species split from its very widespread sister species *V. farnesiana*). Our own research showed that *V. caven* cannot be invasive in the sense of entering and actively degrading sclerophyllous forest and is instead a slow-growing pioneer species and a nurse tree that establishes after disturbance and allows sclerophyllous forest trees to establish via succession (Root-Bernstein et al., 2017b, 2022). However, debates persist around whether *V. caven* is an invasive species in the sense of being of recent anthropogenic origin (Velasco et al., 2023; Root-Bernstein et al., 2017b).

Multi-species rewilding could be scaled up across all of central Chile

The planned corridor project proposed by Sara Larraín fits into our larger vision for scaling the project up across the region. Our full vision would also involve a second corridor of guanaco reintroduction sites in the Cordillera de la Costa that runs up and down the center of Chile (Figure 1). This region, although fragmented by agriculture and roads, also contains some large important conservation areas, for example in in the Man and Biosphere Reserve and National Park La Campana and the National Reserve Las Peñuelas; the Alhué area, Altos de Cantillana Nature Sanctuary, and Palmas de Cocolán National Park; and ideally would extend further south to around San Vicente de Tagua Tagua (where there is an important archeological site) and Santa Cruz (where there are important cultural heritage areas). This potential corridor includes areas with local endemics, and fragmented populations of rare species such as *Jubaea chilensis*. Connectivity between the two mountain corridors can potentially be created through constructing wildlife bridges over the main north-south highway. Rewilding may help to maintain the habitats supporting these species, and restore critical missing ecological functions (see above, *Restoration justification*). It could also allow integrated natural and cultural heritage tourism.

In addition, our vision for species reintroductions or translocations does not stop with guanacos and *V. caven*. Other species that we are interested in potentially seeing translocated, reintroduced, or managed in central Chile in order to bring back ecosystem functions and processes such as fire control, seed dispersal, soil nutrient cycling, shade and soil moisture provision, and so on, includes cattle and horses as proxies for extinct megafauna (including extinct horses), ñandú (rheas) *Rhea pennata*, huemul *Hippocamelus bisulcus* (Flueck et al., 2022), the Chilean palm *Jubaea chilensis*, and trees that should be particularly well adapted to increasing aridity under climate change, such as *Neltuma [Prosopis] chilensis* (Figures 2, 3) Our vision is thus of a mosaic of habitats where currently rare trees that provide ecosystem processes and economic and cultural resources are more abundant due to translocation and restored ecological functions allowing seed dispersal and germination site creation; where guanacos, Darwin's rhea and huemul forage together (Flueck et al., 2022), where cattle

FIGURE 2
Some species that we propose to reintroduce or manage as ecological proxies in central Chile. Top left: A guanaco *Lama guanicoe* released into the Andean foothills (photo MR-B). Top right: An extensively grazed cow in central Chilean woodland (photo MR-B). Bottom left: rhea *Rhea pennata* (photo CHUCAO, CC BY-SA 3.0 <https://creativecommons.org/licenses/by-sa/3.0>, via Wikimedia Commons). Bottom middle: huemul *Hippocamelus bisulcus* (photo: Secretaria de Turismo de Esquel, CC BY-SA 4.0 <https://creativecommons.org/licenses/by-sa/4.0>, via Wikimedia Commons). Bottom right: extensively grazed horses, Palmas de Cocolán National Park (photo MR-B).

FIGURE 3
Some plant species that we propose to manage for conservation and restoration and/or translocate. Left top: *espinos Vachellia [Acacia] caven*, in an early-succession *espinal* (photo: MR-B). Left bottom: Chilean *algarrobo Neltuma chilensis*, Parque Quinta Normal, Santiago (photo: MR-B). Center: native *chañar Geoffrea decorticans*, Parque Quinta Normal, Santiago (photo: MR-B). Far right: Chilean palms *Jubaea chilensis*, Palmas de Cocalán National Park (photo: MR-B).

and horses continue to be allowed to roam freely at low densities, and where pumas and condors are more abundant and primarily feed on guanacos (rather than horses as is now the case).

However, there is no scientific consensus that most the animal species mentioned here belong in central Chilean habitats, partly due to a lack of integration between paleoecology and conservation biology in Chile, and the relatively limited paleoecological and historical data on species distributions (Root-Bernstein et al. submitted). This vision is speculative and generates a series of scientific hypotheses that orient our further research, rather than imposing a pre-determined outcome.

Involvement of local communities is essential

Principles 6, 7, and 10 of the IUCN's principles of rewilding call for engagement with society and local communities (IUCN Rewilding Thematic Group, 2018). Community engagement is also crucial for reintroductions and translocations (Consorte-McCrea and Bath, 2020). We follow Consorte-Crea and Bath's (2020) recommendations through interdisciplinary and social science research and involving local actors in project consultation and co-construction (e.g. Lindon & Root-Bernstein, 2014; Root-Bernstein et al., 2020, 2022; Guerrero-Gatica et al., 2023). Co-construction refers to a set of best-practice processes taking into account gender and other social inequalities, that engages stakeholders in contributing their local or traditional knowledge towards producing new applied knowledge, research hypotheses, and project goals, with high social legitimacy and relevance (Jagannathan et al., 2020; Latulippe and Klenk, 2020). Community conservation, defined as the devolution of decision-making to stakeholders, avoidance of elite capture, the use of standards and regulations to increase accountability, and the inclusion of adaptive learning mechanisms for management (Ribot et al., 2010; Brooks and Waylen, 2012), posits that local people need to be involved in restoration and conservation projects (Berkes, 2004; Brockington, 2004; Danielsen et al., 2007; Brooks and Waylen, 2012). Since early on in the project, we imagined a desirable scenario in which the central Chilean landscape would be more ecologically connected, for example via a regionally self-coordinating system of semi-wild guanaco transhumance (Root-Bernstein et al., 2016; Root-Bernstein and Svenning, 2017). It is vital to safeguard the local ecological knowledge that has been and is still formed through peasant livelihoods (Berkes, 2004; Aswani et al., 2018; Albuquerque et al., 2021).

Integrating sustainably managed traditional resource use may be expected to increase positive perceptions of restoration and conservation initiatives by local populations (Root-Bernstein and Frascaroli, 2016). However, community-based natural resource management projects have a poor record of delivering their social and ecological goals (Kellert et al., 2000; Dressler et al., 2010). The adaptive capacity of relevant institutions may be crucial (Armitage, 2005). Institutional reform is a complex, society-wide issue that may be beyond our direct influence. Moreover, community conservation and community-based natural resource management approaches

TABLE 1 Evaluation of our application of the principles of rewilding, following IUCN Rewilding Thematic Group (2018).

Principle of Rewilding	Description	How we apply this principle	Stage of achievement
1	Rewilding utilizes wildlife to restore trophic interactions	Guanaco reintroduction to browse *V. caven*. We are also interested in other species, and in non-trophic interactions.	Pilot release implemented. Full reintroduction not implemented. Full set of evidence for expected ecological interactions not completed.
2	Rewilding employs landscape-scale planning that considers core areas, connectivity and co-existence.	We have not carried out a formal land use planning study, but we have analyzed connectivity between woodland types and potential for guanaco movements between them. Our vision includes protected areas, landscape connectivity, and co-existence with humans (Figure 1).	Land use planning study not implemented. Land use plan not implemented.
3	Rewilding focuses on the recovery of ecological processes, interactions and conditions based on reference ecosystems.	We are currently developing historical and paleoecological baselines for reference ecosystems. We hypothesize that guanacos (and other species) can contribute to ecological processes such as fire control, seed dispersal, nutrient transport and recycling, shade and soil moisture retention.	Baselines from reference ecosystems not completed. Study of recovery of ecological processes in progress. Recovery of ecological processes not implemented.
4	Rewilding recognizes that ecosystems are dynamic and constantly changing.	We are not committed to compositionalist values.	Our commitment to this principle is ongoing and guides our work.
5	Rewilding should anticipate the effects of climate change and where possible act as a tool to mitigate impacts.	We have not worked explicitly on this issue at this time.	Not implemented.
6	Rewilding requires local engagement and support.	We use a co-production approach and work with local ecological knowledge. Our strategy involves developing broad social consensus. We engage in outreach to the public through social media, magazine and newspaper articles, participation in local festivals, etc. We have support from a broad range of stakeholders and actors.	Local engagement and support are in progress.
7	Rewilding is informed by both science and indigenous and local knowledge.	We use a co-production approach and work with local ecological knowledge. We actively produce scientific hypotheses and research to better understand social and ecological aspects of the context.	Some scientific studies have been completed. Other scientific studies have not been completed or started. Co-production of knowledge working with local ecological knowledge holders is ongoing.
8	Rewilding is adaptive and dependent on monitoring and feedback.	We were not able to fund monitoring of the pilot reintroduction.	Not implemented.
9	Rewilding recognizes the intrinsic value of all species and ecosystems.	We draw on intrinsic values of nature, as well as other values and justifications, some of which are anthropocentric.	Informs our ongoing work.
10	Rewilding requires a paradigm shift in the co-existence of humans and nature.	We work towards "providing optimism, purpose and motivation" by circulating our vision of how central Chile could be in the future, in ways that imply a paradigm shift. We have generated a shared consensus around certain issues and public fora for debate about guanaco rewilding. Our engagement with controversies can be seen as contributing to transformative change (Skrimizea et al., 2020).	Informs our ongoing work. Not achieved.

lack clear theories of change or hypotheses that could help identify leverage points (Root-Bernstein, 2020) and are rarely properly evaluated especially when they fail (Catalano et al., 2019), factors that together reduce learning opportunities that we can draw on. Due to the lack of best-practice guidance, and the bottom-up nature of a co-construction approach, we do not currently know exactly what form community conservation will take in our project. Despite these uncertainties, we believe that the risk of failure of community-based natural resource management is justified on ethical grounds, as an aspect of environmental and social justice (i.e. access to traditional peasant livelihoods) (Martínez Alier, 2002; Dressler et al., 2010; Kay, 2014).

In the context of our collaboration with the Cascada de las Ánimas Nature Sanctuary, we have begun to engage with the local community in order to co-produce an approach to rewilding in the area (Guerrero-Gatica et al., 2023). In our initial vision, which will be modified through co-production/co-construction methods, local people would be legally permitted to sustainably harvest natural resources, and to carry out traditional management practices. Access to land on which these practices can be carried out can be obtained through agreed management plans on public and private lands, and through strengthening and negotiating traditional access rights. Adaptively managed traditional management practices (Berkes, 2004) may also help to replace the missing ecosystem processes of extinct megafauna for which there are no other realistic proxies (Root-Bernstein and Ladle, 2019). Ideally these harvesting and managing practices would be carried out through bottom-up collective action, much as they were in the past (Moyano Altamirano, 2014; MR-B unpublished material). The shearing of guanaco fiber could also be managed by local collectives. When population sizes of reintroduced animals are large enough, regulated hunting could be allowed. We are also interested in investigating whether it would be a good idea to promote llama or alpaca raising, which is rare in central Chile, but which might provide many of the same ecological functions as guanacos, in contexts where it is impractical to introduce wild camelids.

Communities are not uniform (Titz et al., 2018) and social life involves tensions (e.g. Le Billon and Duffy, 2018). There is always a risk of social tensions associated with every conservation, restoration, and rewilding project. Engaging in co-construction and community conservation may reduce but does not eliminate the risk of social tensions associated with a project. Projects can cause conflicts, but they may also be lightning rods for the expression of pre-existing tensions and conflicts (e.g. Krauss, 2005; Douglas and Veríssimo, 2013). As Bourdieu has pointed out, it is not possible for everyone to always perform socially in a way that no one can criticize (Bourdieu, 2018). Negotiating the variety of conflicts that may arise during a long term project is an art.

Evaluation of our project and vision

There are multiple frameworks that could be used to assess the success of a rewilding project (Beyers and Sinclair, 2022; Root-Bernstein, 2022). A process-based rather than outcome-based assessment consists of evaluating how we meet the principles for rewilding as described by the IUCN (IUCN Rewilding Thematic Group, 2018; Carver et al., 2021). The IUCN working group on rewilding gathered input from a variety of rewilding researchers and practitioners around the world, including a representative of Kintu (MR-B), to come up with a consensus list of rewilding principles. Although not all rewilding projects necessarily conform to these principles, we are satisfied by the principles and find them appropriate to apply to our own project. We assess how we meet these principles in Table 1. From an outcomes perspective, the project is innovative within its context, and thus has a very high risk of failure. Objectively, we have none of the resources that characterize successfully implemented rewilding projects, such as control over a large landholding and budget (Root-Bernstein et al., 2018), and we have not advanced beyond a proof-of-concept pilot reintroduction. On the other hand, vision-led rewilding projects are often able to overcome hurdles and setbacks (Root-Bernstein et al., 2018; but see Theunissen, 2019). Optimism and hope are part of our strategy and vision. A successful aspect of our strategy has been to circulate speculations, arguments, hypotheses and evidence about how the central Chilean landscape could be restored. This has resulted in identifying a range of collaborators and stakeholders who share our vision and are interested in testing our hypotheses, and whose capacities complement ours.

Finally, it almost goes without saying that this is not a top-down vision that we will impose on local people, and that our commitment to safeguarding the value of local ecological knowledge and local management traditions imply a co-production approach to the project (Jagannathan et al., 2020; Norström et al., 2020; Guerrero-Gatica et al., 2023). The project depends entirely on the building of a broad consensus for a shared vision (which undoubtedly will be a modification of our current vision) and on diverse local actors helping to overcome our lack of capacity by taking the initiative and making the project their own.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

MR-B: Conceptualization, Writing – original draft, Writing – review & editing. MG-G: Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1441980/full#supplementary-material

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Monitoring terrestrial rewilding with environmental DNA metabarcoding: a systematic review of current trends and recommendations

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Introduction: Rewilding, the facilitation of self-sustaining and resilient ecosystems by restoring natural processes, is an increasingly popular conservation approach and potential solution to the biodiversity and climate crises. Outcomes of rewilding can be unpredictable, and monitoring is essential to determine whether ecosystems are recovering. Metabarcoding, particularly of environmental DNA (eDNA), is revolutionizing biodiversity monitoring and could play an important role in understanding the impacts of rewilding but has mostly been applied within aquatic systems.

Methods: This systematic review focuses on the applications of eDNA metabarcoding in terrestrial monitoring, with additional insights from metabarcoding of bulk and ingested DNA. We examine publication trends, choice of sampling substrate and focal taxa, and investigate how well metabarcoding performs compared to other monitoring methods (e.g. camera trapping).

Results: Terrestrial ecosystems represented a small proportion of total papers, with forests the most studied system, soil and water the most popular substrates, and vertebrates the most targeted taxa. Most studies focused on measuring species richness, and few included analyzes of functional diversity. Greater species richness was found when using multiple substrates, but few studies took this approach. Metabarcoding did not consistently outperform other methods in terms of the number of vertebrate taxa detected, and this was likely influenced by choice of marker, sampling substrate and habitat.

Discussion: Our findings indicate that metabarcoding, particularly of eDNA, has the potential to play a key role in the monitoring of terrestrial rewilding, but that further ground- truthing is needed to establish the most appropriate sampling and experimental pipelines for the target taxa and terrestrial system of interest.

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environmental DNA, eDNA, biodiversity monitoring, terrestrial, rewilding, DNA-based monitoring

Introduction

Rewilding has become an increasingly popular approach to the large-scale recovery of nature, with an aim to restore ecosystems to the point that they are self-sustaining and resilient, with increased trophic and functional complexity (Fernández et al., 2017; Carver et al., 2021; Pettorelli and Bullock, 2023). Rewilding can include species translocations, land abandonment ('spontaneous rewilding'), and actions which actively kick-start ecological processes, followed by minimal intervention (Perino et al., 2019; Carver et al., 2021). These approaches can be applied across a range of ecological, spatial, temporal, and societal contexts, though are applied mainly to terrestrial ecosystems (Prior and Brady, 2017; Carver et al., 2021).

Literature surrounding rewilding is often disjointed, sometimes contradictory, frequently dominated by opinion pieces, and there is a lack of empirical, quantitative data and research (Pettorelli et al., 2018). A key goal of rewilding is to restore ecosystem processes and functioning, therefore monitoring strategies need to focus on the ecological integrity of whole ecosystems, in particular measuring trophic complexity, disturbance regimes and landscape connectivity (Torres et al., 2018). In comparison to more established restoration approaches, rewilding impacts can be unpredictable, forming potentially novel ecosystems over unknown timescales (Pettorelli and Bullock, 2023). For the purposes of this paper, we view rewilding and restoration as related but distinct conservation approaches. As both Mutillod et al. (2024) and Nelson (2022) note, whilst they may share the same ultimate goal, the ways to get there and the visions of what recovery looks like are different. While both seek to restore damaged ecosystems, rewilding generally focuses more on letting nature take its course once initial interventions are made. Rewilding also tends to lack historical benchmarks with which to measure a project's success, unlike restoration (du Toit and Pettorelli, 2019). This inherent indeterminacy necessitates continuous monitoring strategies to understand impacts over long timescales, ideally with an adaptive management approach to help determine the level of any ongoing interventions or management decisions (Perino et al., 2019; Carver et al., 2021). Comprehensive and cost-effective monitoring methods, which maximize taxonomic coverage across different groups of organisms and can be applied at multiple spatial and temporal scales, are essential to understand whether rewilding practices are effective. Monitoring can also minimize any associated risks such as uncertainty around reintroductions, particularly for taxonomic substitutions of extinct native species, and uncertain timeframes, helping to enable the wider implementation of rewilding into legislation and policy (Pettorelli et al., 2018). However, questions remain regarding the best monitoring approach to cover a breadth of taxonomic diversity across temporal and spatial scales, and whether a holistic approach, integrating multiple methods may be most suitable in the context of rewilding.

In the last decade, biodiversity monitoring has experienced a molecular revolution, largely as a result of advances in high-throughput sequencing of PCR amplified gene regions ('barcodes') of interest across multiple taxa; a method known as 'metabarcoding' (Lawson Handley, 2015; Creer et al., 2016; Deiner et al., 2017; Takahashi et al., 2023). Metabarcoding has been applied to a number of mixed sample types, including bulk samples of invertebrates (often referred to as invertebrate "soup" e.g. Yu et al., 2012), ingested DNA from feces of predators or herbivores (sometimes described as 'biodiversity capsules' (Boyer et al., 2015; Nørgaard et al., 2021) or invertebrate-derived DNA ('iDNA', i.e. samples of blood meals of leeches or biting insects (Schnell et al., 2012, 2015; Abrams et al., 2019; Siegenthaler et al., 2019; Drinkwater et al., 2021a, 2021b). However, arguably the greatest sea change in metabarcoding of biodiversity over the last decade has been the analysis of environmental DNA or 'eDNA' (Taberlet et al., 2012; Creer et al., 2016; Deiner et al., 2017; Pawlowski et al., 2021; Takahashi et al., 2023), catalyzed by publication of a seminal paper describing how eDNA metabarcoding of seawater can effectively recover information on marine fish communities (Thomsen et al., 2012). Environmental DNA is DNA released by organisms into their environments via shed cells, mucus, gametes, and waste or decaying material, in addition to DNA from whole microbial and meiofaunal taxa present in environmental samples (Taberlet et al., 2012; Pawlowski et al., 2021). Although water and soil are the most common substrate types for sampling eDNA, eDNA metabarcoding studies have also been successfully performed on diverse sample substrates including snow (Kinoshita et al., 2019), air (Clare et al., 2022; Lynggaard et al., 2022) saltlicks and drinking water vessels (Ishige et al., 2017), spider webs (Gregorič et al., 2022), swabs and tree-roller samples (Allen et al., 2023). eDNA metabarcoding is particularly promising as a tool for non-invasive monitoring of rewilding across ecosystems and different spatial scales, as it has potential to generate whole-community datasets across the tree of life, estimate standard community and functional diversity metrics and perform trophic network analysis (Yan et al., 2018; Meyer et al., 2020; Blackman et al., 2022; Condachou et al., 2023; Hassan et al., 2023). To date though, there has been a much greater emphasis on eDNA metabarcoding for monitoring of aquatic than terrestrial ecosystems (van der Heyde et al., 2022).

Guidelines are needed for translating DNA metabarcoding into practice, and improving its uses in biodiversity monitoring (Blackman et al., 2024), particularly in terrestrial contexts (van der Heyde et al., 2022), which are generally more diverse and heterogeneous over smaller spatial scales than aquatic environments (Grosberg et al., 2012). Firstly, choice of sampling substrates can strongly influence the detection of different taxa (van der Heyde et al., 2020), but little guidance exists on the best substrate choice for different taxonomic groups, and it is unclear whether sampling multiple substrates is necessary or worth the increased effort and resources (van der Heyde et al., 2020, 2022). Secondly, a meta-analysis has demonstrated that eDNA metabarcoding often outperforms traditional methods in terms of cost, sensitivity and number of species detected (Fediajevaite et al., 2021), but this might reflect a bias towards aquatic systems and substrates, as well as a publication bias (failures may be less likely to be published; Beng and Corlett, 2020). The limited comparisons of metabarcoding and traditional methods in terrestrial settings so far indicate performance is mixed, both in terms of sensitivity and species detected (Fediajevaite et al., 2021), and questions therefore remain about the most suitable approach.

Here, we systematically review applications of metabarcoding to monitoring biodiversity in terrestrial ecosystems, focusing on eDNA, but also including relevant studies that have used bulk invertebrate or ingested DNA samples (i.e. fecal samples *or* iDNA). Our aim is to help inform how metabarcoding, in particular of eDNA, can be integrated into monitoring of terrestrial rewilding as well as other terrestrial conservation practices. We address the following research questions: 1) what are the trends in publications of terrestrial metabarcoding in relation to geographic location, target organisms, sample substrates used, and types of analyses performed to understand community or functional diversity?; 2) which sample substrate(s) are the most appropriate for the different target organisms and how does the sampling of multiple substrates affect the number of species detected and taxonomic coverage?; 3) how does metabarcoding perform when compared to traditional monitoring methods for terrestrial target taxa, and is this comparison dependent on choice of sampling substrate, the choice of target region and primer pairs for metabarcoding, and/or taxonomic focus?; and 4) what are the research gaps we need to fill for eDNA metabarcoding to be routinely used for effective monitoring of rewilding?

Materials and methods

Literature search

We performed a systematic review, using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (https://www.prisma-statement.org/, Supplementary Figure S1). A literature search was conducted in Scopus and Web of Science to ensure the greatest coverage of journals relating to Natural Sciences (Mongeon and Paul-Hus, 2016) on 3rd January 2024. Initially, a search of the terms '*eDNA* OR *Environmental DNA* OR *metabarcoding*' AND '*rewild**' was performed. This only returned 12 relevant studies, the majority of which focused on herbivore diet composition, indicating the so far limited application of DNA metabarcoding to monitor rewilding. To supplement these papers we performed a second, broader search to identify published scientific studies which used metabarcoding of environmental DNA to monitor terrestrial communities, with the aim that this would better show the potential applications for rewilding monitoring. This second search consisted of the following terms: '*eDNA* OR *Environmental DNA* OR *metabarcoding*' AND '*trophic* OR *function** OR *network*' OR '*monitor** OR *survey**'. Results were then refined to include terrestrial studies only, using the addition 'AND (*terrestrial*)' term. The *trophic* OR *function* OR *network* search term was included to capture studies that have performed additional functional analyses beyond species richness or community comparisons.

Studies that sampled bulk DNA from invertebrates, were also included, as well as DNA from feces of predators or herbivores or iDNA. Fecal and iDNA samples were combined in the present study in the category 'ingested' DNA. Substrates that appeared less than three times in the database (e.g. spider webs, saltlicks, snow) were categorized as 'Other'. Definitions of all substrates included are provided in Supplementary Table S1.

The automated refinement tools within Scopus and Web of Science were used to remove irrelevant studies (e.g. those from other disciplines such as Psychology, Physics etc.) and reviews or perspectives. After removing duplicates, this output was manually screened so that it included studies focusing on contemporary terrestrial ecosystems, at least in part (i.e. not wholly aquatic-focused, ancient DNA, or lab/desk-based studies where samples were not collected directly from the field). Of the remaining studies, further refinement removed papers which only used a single-species approach (quantitative PCR, droplet digital PCR etc.), leaving 164 papers analyzed in this review. This final refinement process enabled us to focus on papers with a community or ecosystem approach, which is important in the context of monitoring impacts of rewilding.

To understand the publication trends of these results in the context of the wider field of eDNA and DNA metabarcoding, we collected a list of papers from a search using only '*eDNA* OR *Environmental DNA* OR *metabarcoding*' and a second search adding 'AND *soil*' from both Web of Science and Scopus. We were then able to look at the proportion of papers and overlap of those included in the current study compared to those with potentially more aquatic or below-ground focuses.

Data extraction and analysis

The following details were recorded from each publication: the study's target taxa; primers used; substrates sampled; the ecosystem from which samples were taken; and analyses performed (see Supplementary Tables S1–S3 for definitions). Data analysis and visualization were undertaken using R version 4.3.1 (R Core Team, 2023) in RStudio version 2024.04.0 (Posit team, 2024), with the packages dplyr (Wickham et al., 2023a), tidyr (Wickham et al., 2023b) and tidyverse (Wickham et al., 2019) for data handling and ggplot2 (Wickham, 2016); hrbrthemes (Rudis, 2020) and viridis (Garnier et al., 2023) for visualization. To investigate publication trends (research question 1), a Sankey diagram was created using ggsankey (Sjoberg, 2023), and geographical trends plotted using ggplot2 (Wickham, 2016) and sf (Pebesma and Bivand, 2023) packages.

To investigate which substrate(s) are appropriate for chosen taxa and whether sampling multiple substrates improves taxonomic coverage (research question 2), information on taxonomic richness detected for each substrate was collected from articles which used multiple substrates for sampling. UpSet plots were created using UpSetR (Gehlenborg, 2019) to visualize the preference for multiple substrate and taxa combinations across studies. Pairwise comparisons for different substrate combinations were then analyzed to determine relative performance. The proportion of unique taxa detected only with one substrate, and the proportion of taxa shared between both substrates was calculated to allow comparisons across studies and visualized using stacked barcharts. Where a study sampled different sites that were treated separately in their own analyses, these were treated as independent comparisons. Similarly, where a study used more than two substrates, each pairwise comparison between substrates was treated independently. For each study, data was collected for the lowest taxonomic rank available across both methods so that data remained comparable.

A comparison of metabarcoding and traditional methods (research question 3) was carried out for vertebrates only, since just two studies compared metabarcoding with traditional methods from non-vertebrate taxa. Fifteen studies compared metabarcoding and traditional monitoring for detection of vertebrates. Our analysis focused on the influence of three variables: substrate choice, amplification/primer region, vertebrate focus. The data from these studies were expanded by treating discrete sites within each study separately, resulting in a dataset of 32 comparisons. We also treated individual substrates, primer regions or vertebrate focuses separately, providing a total of 33, 36 and 46 pairwise comparisons for analysis. Here 'traditional' monitoring methods, included camera traps or field surveys [e.g. line transects (Coutant et al., 2021), trapping (Mena et al., 2021) or vegetation surveys (Edwards et al., 2018)]. The proportion of unique taxa compared to total taxonomic richness was plotted for each comparison of metabarcoding *vs* traditional methods. Wilcoxon signed-rank tests were used to compare the median proportion of taxonomic richness between metabarcoding and traditional methods for the comparisons of different substrate, primer region and taxa in addition to overall comparisons of metabarcoding with cameras, and metabarcoding with field surveys.

Results

Database and publication trends

After refinement, 164 of the 299 studies identified were retained for analysis. The number of metabarcoding studies increased markedly between 2013 and 2023, from 54 to 962 (Figure 1A). The number of terrestrial metabarcoding studies has increased over time (Figure 1B) but they made up a small proportion (<20%) of the total, and this proportion has not increased over time (Figure 1A). Soil-focused studies ranged from 10-16% of all metabarcoding studies over the last 10 years (Figures 1A, B), while other terrestrial metabarcoding studies remained between 2-4% of the total. Of the studies included in our further analyses, 69% were based on eDNA metabarcoding, with the remaining 31% sampling ingested DNA or bulk invertebrates.

Terrestrial metabarcoding studies have been conducted on all continents, but with a bias towards Europe (n= 58 studies) and North America (n=34 studies) (Figure 1C). By country, most studies have been conducted in the USA (n=19), Denmark (n=13), China (n=9 and Germany (n=8) while no studies have been conducted in most African countries or in the Middle East (Supplementary Figure S2). Studies spanned diverse ecosystems, including urban, riparian, polar, peatland, grassland, coastal, alpine and agricultural habitats, but the most targeted ecosystem was forests, with over one third of papers (66 studies) sampling only in forests or woodlands. Only 21 studies (13%) sampled multiple ecosystems, and all these included forest ecosystems.

Soil, water and ingested material were the most common substrate choices for metabarcoding analysis in terrestrial ecosystems, with 34% of studies sampling soil (n=39 only soil, plus 16 using soil alongside other substrates), 24% sampling ingested material (n=39 only ingested material, plus one with other substrates, and 21% sampling water (n=27 only water, plus seven using water alongside other substrates), Figure 1B; Supplementary Figure S3A). Sampling of all substrates has increased over time, with the notable addition of air and surface swabs since 2022 (Supplementary Figure S3A). Only 10% of studies sampled multiple substrates (n=17, Figure 2A), and 5 of these studies were in 2023. Of these studies, six (35%) sampled both water and soil, four (24%) sampled soil and plant material, and two (12%) sampled soil and surface swabs (Figure 2A). The maximum number of substrates was four (soil, ingested material, plant material and bulk invertebrates), sampled in a single study (Figure 2A).

Vertebrates, invertebrates and fungi were frequently studied, with vertebrates studied in 37% of studies (n=47 vertebrate only, plus 13 with a multi-taxa focus), invertebrates in 33% (n=35 single plus 16 multi-taxa) and fungi in 28% (n=23 single, plus 23 multi-taxa, Figures 1C, 2B). Only ten studies focused just on plants, though a further 11 included plants as part of broader taxonomic surveys. Overall, 21% of studies (n=35) had a multi-taxa focus, with eight of those studies carried out between 2022-2023. Across these 35 studies there were 19 different taxonomic combinations, (Figure 2B), with no clear consensus over choice of combination.

The majority (57%) of studies investigated species richness and community composition only (n=93, Figure 1C). Twenty-four percent of studies carried out network analyses (n=32 one analysis type, plus n=8 multiple analyses), and a further 21% assigned functional groups (n=26 one analysis type, plus n=8 multiple) (Figure 1C). Three studies estimated functional diversity metrics, and just a single study on invertebrates investigated genetic diversity (Figure 1C; Supplementary Figure S3E). Network analyses were carried out on all taxa, though functional group assignment was mainly carried out for fungi, invertebrates, bacteria and archaea, rarely for vertebrates and protists, and not for plants (Supplementary Figure S3E). Three studies performed network analyses across multiple taxonomic groups, though just one included vertebrates, invertebrates and plants in this analysis.

Which substrate(s) are appropriate for chosen taxa and does sampling multiple different substrates improve taxonomic coverage?

Soil samples were used for analyzing all taxonomic groups while water samples targeted all taxa apart from protists, and plant material and air DNA targeted all taxa apart from archaea (Figure 1C; Supplementary Figure S3D). Surface swabs and ingested DNA were used to target invertebrates and vertebrates only. Invertebrates were targeted with all sample types. Vertebrates were targeted with all sample types apart from bulk samples (though iDNA from invertebrates was used, categorized under 'ingested'), with water, ingested DNA, soil, and airDNA being popular (Figure 1C; Supplementary Figure S3D). Fungi and bacteria were sampled mainly via soil, but also commonly through plant material and water. There are few clear trends in terms of which substrates are targeted for certain taxa, apart from a slight trend for vertebrate studies to sample water and fungi studies to target soil (Figure 1C; Supplementary Figure S3D).

Seventeen studies (10%) sampled more than one type of substrate, with the most common substrates used together being soil and water (7 studies), and soil and plant material (4 studies; Figure 2A). Most studies that utilized more than one substrate for sampling found a greater species richness overall. All but five of the 29 comparisons found additional unique taxa with the addition of a second substrate (Figure 3). Soil performed poorly compared to bulk invertebrates, scats, water, plant material and roller swabs in terms of the number of unique taxa identified (Figure 3). For vertebrates, scat sampling performed best overall, with water and roller swabbing also outperforming soil (Figure 3). For invertebrates, scats, plant material and bulk invertebrates all outperformed soil, whereas bulk invertebrates also outperformed plant material and scats, and spray aggregations detected more unique taxa than roller swabs (Figure 3). For bacteria and fungi,

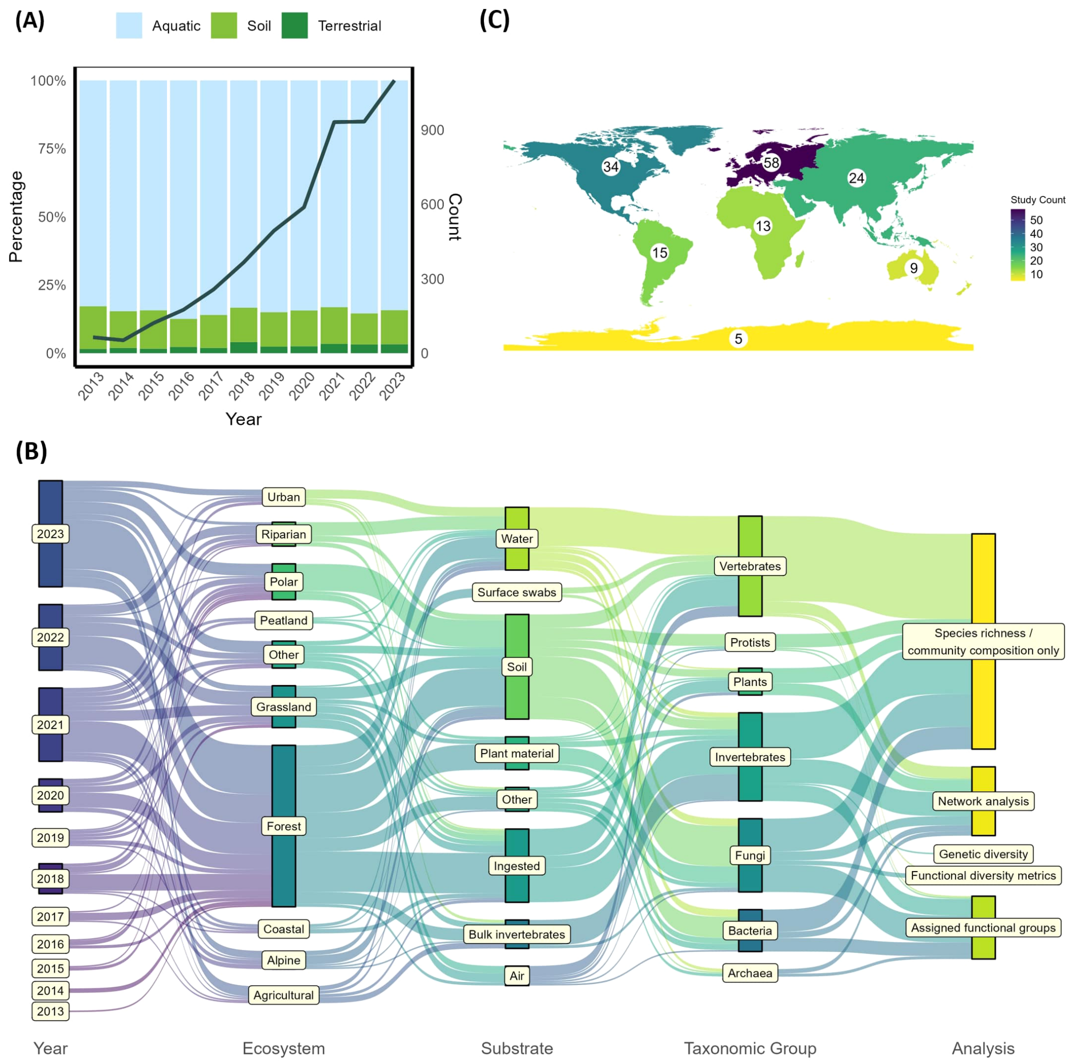

FIGURE 1
Publication trends: **(A)** the number of studies published each year and proportion for terrestrial-focused studies (those included in this review), soil-focused studies and all other eDNA focused-studies (aquatic) according to the Scopus and Web of Science outputs. **(B)** The number of studies by Continent – where samples were taken rather than research institutions. **(C)** Sankey diagram showing publication year, ecosystem sampled, substrate sampled, taxonomic focus and type of downstream analysis for each study. Where a study used multiple substrates or taxonomic groups, each substrate/taxa was counted independently. Substrates with < 3 occurrences were assigned 'Other'. Where a study had multiple focuses per category (e.g. 2 different substrates), these were treated independently to show all interactions.

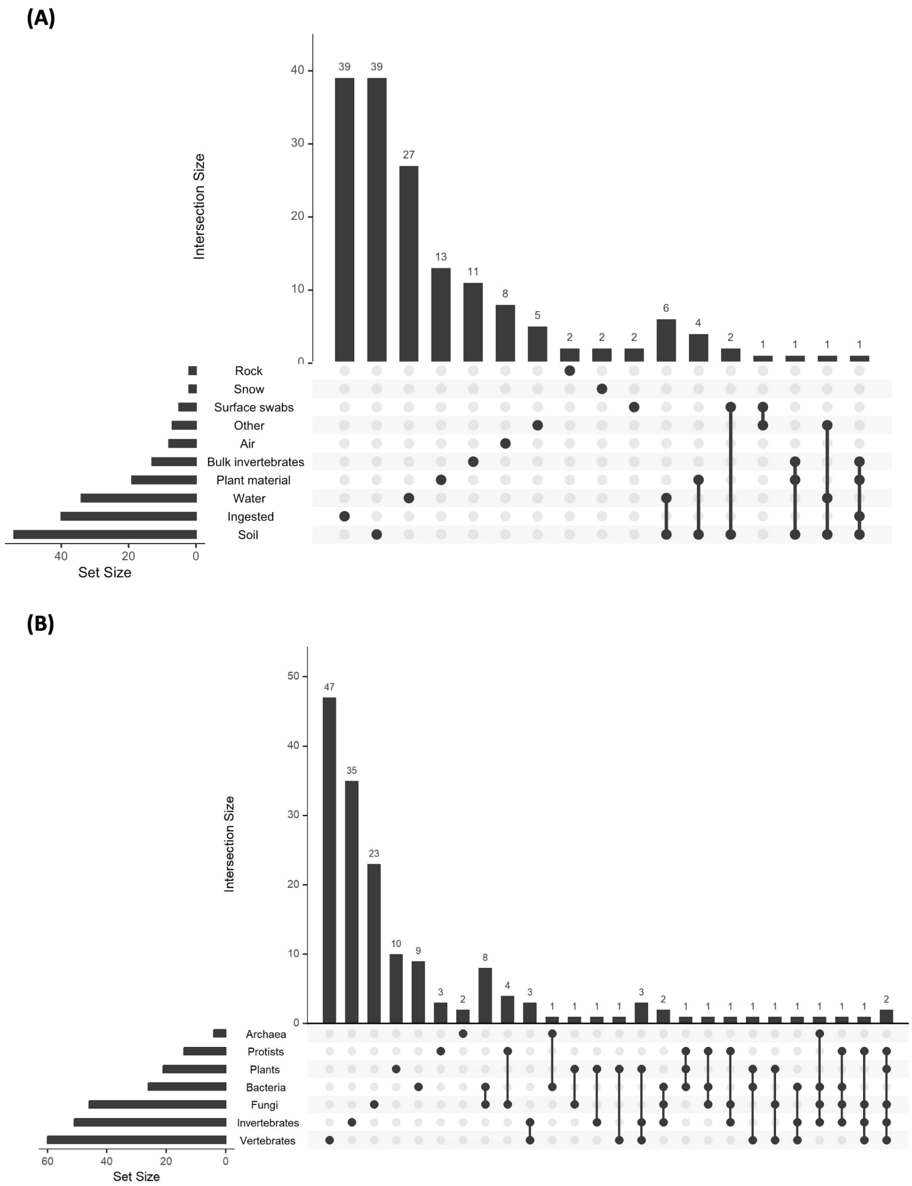

FIGURE 2
Upset plots showing the combinations of **(A)** multiple substrates and **(B)** multiple taxonomic focuses across studies. Intersection size represents the number of studies which focused on the combination represented below each bar. Set size indicates the total number of studies which included a focus on the corresponding substrate or taxonomic group to the right of each bar.

there were more shared and fewer unique taxa overall, but slightly more unique taxa were detected with water compared to soil, and with soil compared to plant matter (Figure 3).

How does metabarcoding perform when used alongside traditional methods for terrestrial vertebrate taxa?

Of the 33 comparisons of DNA-based and traditional monitoring, 13 found a greater proportion of vertebrate taxonomic richness (i.e. more unique taxa) with metabarcoding compared to the traditional method, 15 studies found higher taxonomic richness with the traditional method, and five studies found no clear difference (a difference in proportions of < 10%, Figure 4A). Three quarters of these comparisons were made between metabarcoding and cameras. Eight of these found a higher proportion of unique taxa with metabarcoding, 12 found a higher proportion with cameras, and four found similar proportions between the two. Of the eight comparisons between eDNA and field surveys, four found more unique taxa with eDNA, two found more unique taxa with field surveys, and one study found all the targeted taxa with both methods. No significant differences were found between the proportion of taxa uniquely detected with metabarcoding and either camera trapping or field surveys (Supplementary Table S4).

Half of the comparisons between water-derived eDNA and traditional methods detected more unique taxa with eDNA, while

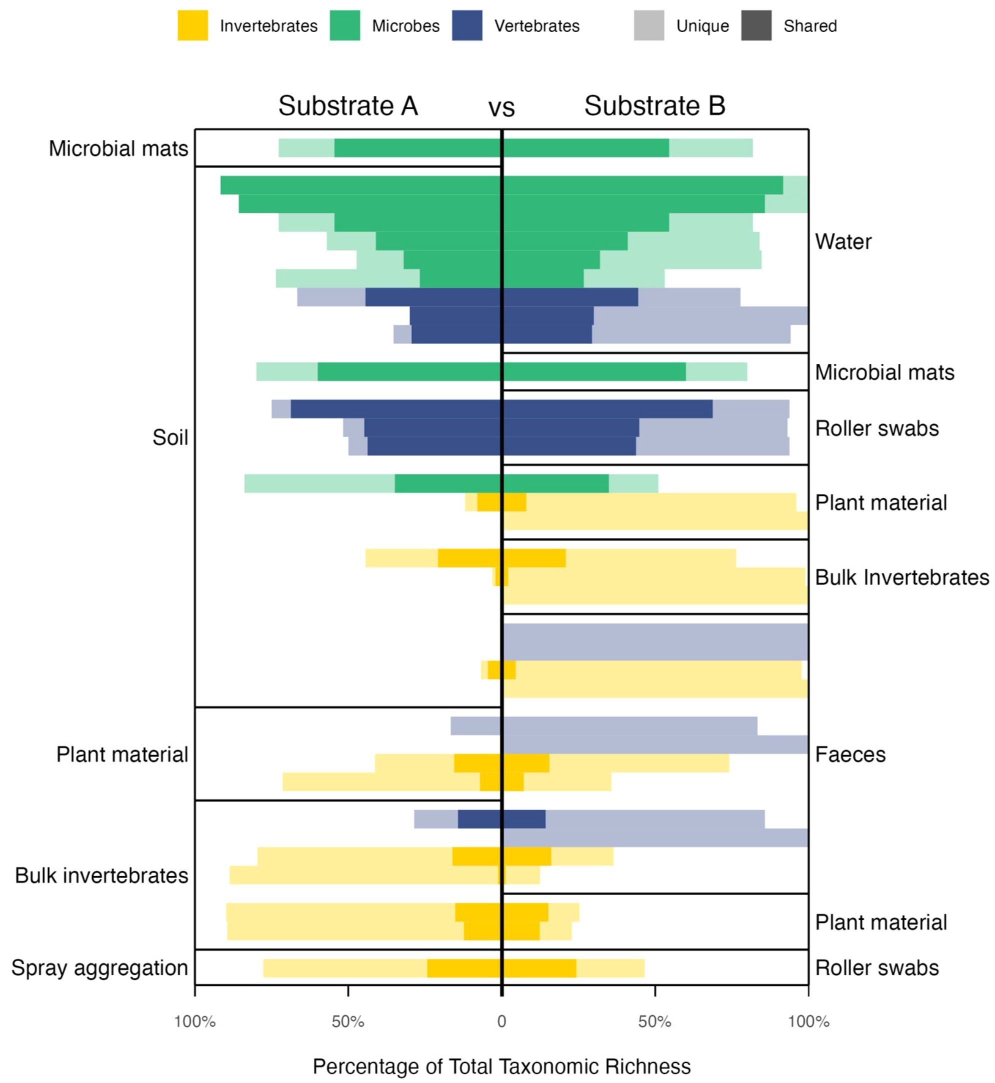

FIGURE 3
Pairwise comparisons of different eDNA substrates, showing the percentage of unique taxa found in each substrate (lighter shades) and the percentage of taxa shared by both substrates (darker shades). Percentages are of the total taxonomic richness when both substrates were combined within each study. Bars are colored according to the taxa detected.

five detected more unique taxa with traditional methods, though no statistical difference was found (Figure 4A; Supplementary Table S4). With iDNA and soil, two of nine studies and one of three studies detected more unique taxa with metabarcoding respectively (Figure 4A), though again, no statistical difference was detected (Supplementary Table S4).

Of the 20 comparisons that used only the 12S rRNA region for vertebrate metabarcoding, 10 detected more unique taxa with metabarcoding, six detected more unique taxa with traditional methods and four studies reported similar taxonomic richness (Figure 4B). By contrast, only two of the 11 comparisons using only 16S reported higher taxonomic richness with metabarcoding (Figure 4B), with this being the only statistically significant difference we detected across all comparisons (n=11, v=7, p=0.019). Five studies included both 12S and 16S, and of these only two comparisons reported higher taxonomic richness with metabarcoding (Figure 4B).

Thirty of 45 pairwise comparisons targeted mammals, and of these, 13 found a higher number of unique taxa with metabarcoding, 11 detected more taxa with traditional methods, and six found no difference (Figure 4C). Two of the 10 studies that detected birds found more unique taxa with metabarcoding, while seven detected more taxa with traditional methods. The two reptile studies both found higher taxonomic richness for traditional methods. Of the three amphibian studies, one found higher richness with eDNA and the others found all detected taxa with both methods (Figure 4C). Statistical tests showed no significant differences between these comparisons (Supplementary Table S4).

Discussion

Our systematic review demonstrated how terrestrial systems have been relatively neglected in relation to eDNA metabarcoding

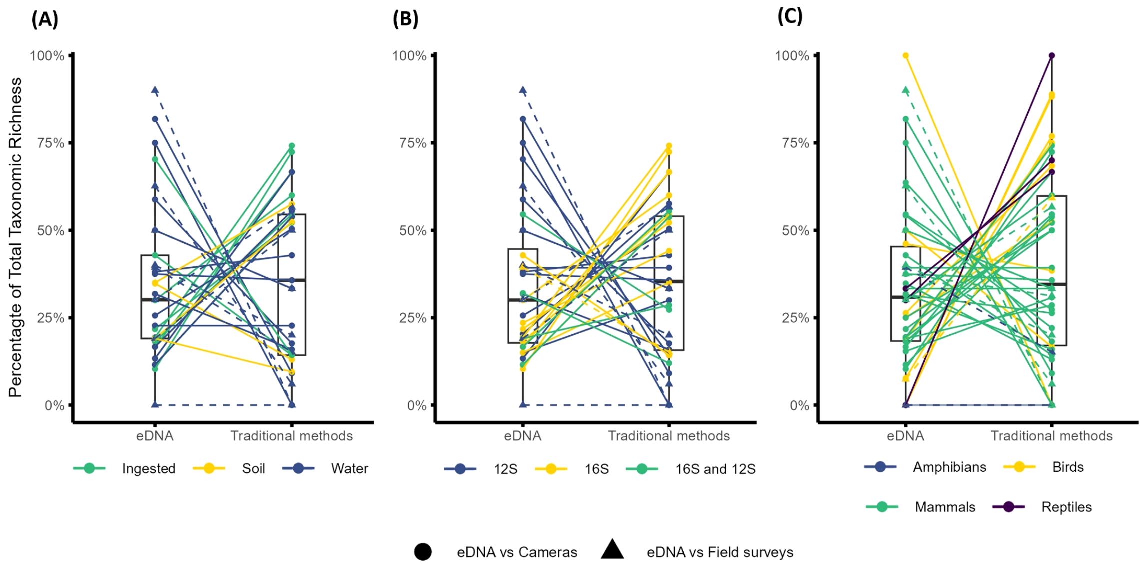

FIGURE 4
The proportion of unique taxa detected with either eDNA or traditional methods, compared to the total taxonomic richness recorded by both methods. Data are only from vertebrate-focused studies. Lines connecting the points indicate the comparable method for each study. Where the traditional method was camera traps, points are circles and lines are solid, other field surveys (e.g. field signs, line transects) have triangular points and dashed connecting lines. The remaining proportion of taxonomic richness which is not plotted is taxa shared across both methods. Where a study sampled multiple different sites, these were treated independently. **(A)** Studies and sites within studies, colored by eDNA sampling substrate (n=32). **(B)** Studies and sites within studies, colored by primer region, with additional data expansion for different amplification regions (n=35). **(C)** Studies and sites within studies colored by the vertebrate taxa detected, with additional expansion of data to separate different taxa (n=45).

research overall. Sixty-nine percent of the 164 studies in our review were based on eDNA metabarcoding, reflecting research emphasis on eDNA as opposed to bulk samples or iDNA. We show that there are current biases towards research effort in the global north, forest habitats and single taxonomic groups (particularly vertebrates), soil as a substrate choice, and descriptive rather than functional analyses. Choice of sampling substrate is highly context-dependent for terrestrial ecosystems, something which has previously been suggested in more specific terrestrial habitats (Kestel et al., 2022; van der Heyde et al., 2022). We found that using multiple substrates in combination improves taxonomic coverage, though substrate choice should be informed by the target taxa. The recent review by van der Heyde et al. (2022) concluded that there is no ‘one size fits all’ approach to ecological monitoring with eDNA, and we draw similar conclusions, suggesting that multi-method ‘toolkit’ approaches, which integrate eDNA with established methods, could be most appropriate approach for future monitoring of terrestrial rewilding.

Publication trends

Although terrestrial metabarcoding studies have increased in number over time, they make up less than 20% of all eDNA metabarcoding studies, and this proportion has remained stable over the last decade, suggesting terrestrial research is lagging behind the field in terms of research effort. In contrast, aquatic eDNA research is maturing from a developmental-focus to more application-focused for ecological monitoring (Schenekar, 2023; Takahashi et al., 2023).

There is also a geographic bias in research coverage, with over 70% of terrestrial eDNA metabarcoding studies conducted in Europe, North America and Asia; a slightly higher proportion than the 61% reported in van der Heyde et al. (2022) which included both targeted and metabarcoding terrestrial studies. A northern hemisphere bias has also been reported for aquatic eDNA studies (DiBattista et al., 2022; Rishan et al., 2023; Takahashi et al., 2023), and highlights the need to promote and support eDNA research in the global south.

Terrestrial metabarcoding studies have been carried out in diverse ecosystems, but by far the greatest emphasis has been on forests and woodlands, with one third of all studies included here sampling these habitats; a similar trend to that noted previously (van der Heyde et al., 2022). This emphasis may be due to the global importance of forest habitats for biodiversity and ecosystem services such as carbon sequestration, as well as their economic importance (Brockerhoff et al., 2017; Coble et al., 2019).

Soil was by far the most sampled terrestrial substrate in our review, featuring in one third of included studies, similar to previous reviews (van der Heyde et al., 2022). Water and ingested material were also popular choices, while more novel methods such as airDNA metabarcoding and surface swabs are increasing in popularity. So far, the use of multiple substrates in terrestrial eDNA studies is limited, with only 11% of the papers combining two substrates and a single study combining four. Combining substrates obviously incurs additional time and resources, so a key question is whether this is worth the effort, which we address in the following section.

Vertebrates, invertebrates and fungi were the most frequently studied taxa in terrestrial systems. Only 20% of studies sequenced multiple taxonomic groups, despite the great potential of metabarcoding to survey across the tree of life (Smart et al., 2016; Stat et al., 2017). This could partly relate to the absence of a 'one size fits all' universal primer combination and the expense of carrying out multiple metabarcoding assays. Functional analyses (beyond species richness and community composition) were often overlooked, as previously documented (van der Heyde et al., 2022), with only ~40% of studies in our review carrying out any network or functional group/diversity analyses. A multi-marker approach, to cover different taxonomic groups, is becoming more feasible and gaining traction, and will create more opportunities for analyses of ecological networks and ecosystem function (Donald et al., 2021; Keck et al., 2022). Nonetheless, only 32% of studies that included multiple taxonomic groups undertook any functional analyses, and only 22% performed network analyzes.

Which substrate(s) are appropriate for chosen taxa and does sampling multiple substrates improve taxonomic coverage?

Environmental DNA from soil and water and ingested DNA (iDNA) were the most common substrates, as mentioned above, and 'soil + water' was the most common substrate combination (n=6). However, the popularity of a substrate does not necessarily reflect its suitability for detecting different taxa. We first reviewed which substrates have been used to target particular taxa, then, based on the small sample of studies (n=17) that have directly compared substrates in terrestrial systems (n=29 comparisons), we asked if certain substrates perform better for particular taxa and whether combining substrates improves taxonomic coverage. As expected, there is no clear 'one size fits all' substrate. Greater species richness was found in the majority (83%) of cases when two substrates were used, compared to the respective substrates in isolation, but whether this is worth the additional cost and effort will depend on the study question, feasibility and taxa of interest.

Soil samples were used for surveying all taxonomic groups, with approximately half of these studies targeting fungi and bacteria, nine (25.7%) targeting vertebrates and three (8.6%) targeting plants. Despite its popularity, soil performed poorly compared to other substrates (water, bulk invertebrates, scats, plant material and roller swabs) in multiple-substrate comparisons, in terms of the number of unique taxa identified, particularly for vertebrates and invertebrates. Performance was however more comparable to other substrates (water, plant material and microbial mats) for microbial taxa. Distribution of eDNA is known to be highly heterogeneous in soil (Hermans et al., 2022), with vertebrate eDNA particularly patchy (Seeber and Epp, 2022; Li et al., 2023). Detection of species of interest can therefore require more extensive sampling and replication, in addition to more costly and/or laborious methods to process sufficient material and overcome inhibitors (such as humic acid) and locate the 'needle in the haystack' (Valentin et al., 2020; Hermans et al., 2022). In addition, eDNA is generally considered to have greater persistence time in soil compared to water and therefore a less contemporary signal, although this is strongly governed by soil properties and where the sample is taken from (Sirois and Buckley, 2019); sampling at the soil surface provides a more contemporary signal of above-ground diversity compared to sampling 20 cm underground (Yasashimoto et al., 2021). Sampling soil is of particular interest for monitoring changes in the communities of below-ground taxa, for example during reforestation. Sampling the upper 10 cm of soil proved effective for detecting changes in soil fungi and bacterial composition over a 30-year chronosequence of reforestation in New Caledonia, for example (Fernandez Nuñez et al., 2021). Soil is arguably less suitable for vertebrates, particularly at landscape scales. For example, soil eDNA (and eDNA more generally) has limited application to terrestrial reptiles (reviewed in Nordstrom et al., 2022), although their detection can be improved by targeted sampling (e.g. under cover objects) and increasing soil volume (Kyle et al., 2022). However, it should be noted that soil eDNA metabarcoding can outperform camera-trapping for mammal detection over relatively local scales (Leempoel et al., 2020), highlighting the importance of considering both scale and taxa of interest.

Water samples were used for all taxonomic groups apart from protists, and over half of the studies that sampled water targeted vertebrates. eDNA detected within a waterbody reflects not only the aquatic and semi-aquatic species living within it, but also the terrestrial species that interact directly with it (through drinking, urinating etc (Harper et al., 2019), or inhabit the surrounding environment. DNA is transported via groundwater run-off and other running water, making it possible to detect species several hundred meters or even kilometers from their location, particularly in lotic environments (Deiner et al., 2016). eDNA metabarcoding of samples from a waterbody is therefore a convenient and effective way to describe the terrestrial biodiversity in a given area (Sales et al., 2020; Broadhurst et al., 2021; Lyet et al., 2021; Mena et al., 2021) and can provide catchment-scale biodiversity measures (Lyet et al., 2021). Sampling water during rainy seasons, when there is increased run-off from soil, can gather data that would otherwise require sampling two substrates (Yang et al., 2021). Water outperformed soil for detection of vertebrates and (to a lesser extent) microbes in our multi-substrate comparisons. Water has also been recommended for terrestrial invertebrate detections (Deiner et al., 2016; Sacco et al., 2022), and better targeted detection of ants was found by sampling water compared to soil with quantitative PCR (Villacorta-Rath et al., 2022) though no studies have yet compared eDNA metabarcoding of water with other substrates for terrestrial invertebrates. Choice of water as a substrate for sampling terrestrial environments of course depends on its accessibility. If permanent water bodies are not present in the site of interest, ponds, puddles, tree rot-holes (Newton et al., 2022), bromeliads (Torresdal et al., 2017) or other ephemeral sources may be appropriate for sampling water.

It is difficult to draw conclusions on the efficacy of other substrates because the number of comparisons is very small. However, roller swabs and feces were effective for sampling vertebrates compared to soil, plant material and bulk invertebrates in pairwise comparisons, while plant material, feces, bulk invertebrates, spray aggregation and (to a lesser extent) roller swabs worked well for invertebrates. Swabbing or rolling tree bark ('tree rolling'), is particularly well-suited to forested habitats for detecting arboreal species, when avian data is a priority (Newton et al., 2022) and/or if water is not readily available for sampling. Fecal samples are also effective for detection of both vertebrate and invertebrate predator and prey (e.g. Harper et al., 2020), but sampling relies on being able to easily locate scats (van der Heyde et al., 2020). Tree-rolling and aggregated water from sprayed leaves (Allen et al., 2022) are promising, non-destructive alternatives to bulk sampling for invertebrates (Roger et al., 2022), but more research is needed to understand their efficacy as so few comparisons have been made. Although airDNA has not yet been included in multi-substrate comparisons, it has great potential to address the 'needle in a haystack' limitation of soil, but conversely may suffer from too great a dilution effect if applied in open spaces (an 'everything is everywhere' problem (Clare et al., 2021, 2022; Lynggaard et al., 2022). Further research is needed to understand the spatial and temporal distribution and dispersion of airborne DNA particles (Clare et al., 2021), but airDNA could be particularly informative when combined with other substrates, to survey different taxa, temporal and spatial scales. Ji et al. (2022) also note the potential for iDNA to enable direct measurements of biodiversity conservation outcomes across protected areas and with broad taxonomic coverage. It is important to stress that choice of substrate(s) depends on the research question, ecosystem(s), and taxonomic group(s) of interest. In the context of rewilding, it may be of interest to detect relatively short-term temporal changes in biodiversity, which requires sampling contemporary eDNA, and it is important to consider that eDNA degrades faster in water (Barnes and Turner, 2016) and on tree bark (depending on weather conditions; Allen et al., 2023).

How does metabarcoding perform when used alongside traditional methods for terrestrial target taxa?

There was large variation in the relative performance of metabarcoding in comparison to traditional methods across studies, which suggests it is highly context dependent, as has been suggested for aquatic sampling (Keck et al., 2022). This is equally apparent when looking closer at substrate choice, though the outcome for eDNA metabarcoding was slightly better when restricted to water versus traditional methods (53% found more taxa with eDNA). Terrestrial vertebrate eDNA can be highly localized in both water (Harper et al., 2019) and soil samples (Andersen et al., 2012) and the detectability of species is dependent on their level of interaction with the substrate and the local environment (Andersen et al., 2012; Ryan et al., 2022). Water samples are more likely to detect species with a high affinity to water, compared to traditional methods that may be better suited to detect fully terrestrial or arboreal species (Coutant et al., 2021; Mena et al., 2021). This is particularly important for amphibian monitoring, as species may become less detectable with aquatic eDNA after shifting to their terrestrial life-stage, highlighting the importance of the timing of sampling (Moss et al., 2022).

We found that the 12S region performed better than the 16S region in terms of unique taxa detected when compared to traditional methods. Seventy percent of 20 studies employing 12S found similar or higher taxonomic richness compared to traditional methods, whereas only 18% of 11 studies found higher richness with 16S. Targeting both these regions in combination has been widely recommended to increase taxonomic coverage (Kumar et al., 2022; Siziba and Willows-Munro, 2024). Despite this, only two of the five comparisons that employed both markers found higher taxonomic richness with eDNA. Our findings might therefore suggest that 12S is a better choice for maximizing taxonomic coverage of vertebrates, and that there is little to gain from also including 16S. However, this result is likely influenced by the choice of different primers for the two regions, amplicon length, reference database coverage, and other features of the study design. In a recent direct comparison, newly designed vertebrate primers for 16S outperformed 12S and COI primers in terms of detection, amplifying 98% of vertebrate species included in *in silico* tests (Wang et al., 2023). This study also found improved species detection with multiple markers and highlighted the complementary nature of the three regions (Wang et al., 2023), therefore we caution against dismissing 16S based on the small number of comparisons included here.

Finally, we found mixed results in the relative performance of methods in terms of the vertebrate taxa they detected, though there is some suggestion that traditional methods may remain a more favorable choice for bird and reptile monitoring. Low DNA shedding rates due to the keratinized exterior of reptiles may reduce their detectability in environmental samples (Adams et al., 2019; Andruszkiewicz Allan et al., 2021). Likewise, the diversity and life-histories of taxa may influence detectability. Flying species, in addition to solitary, large-ranging species such as carnivores, may have limited interactions with terrestrial sampling substrates and therefore tend to be better detected with camera traps or field surveys (Leempoel et al., 2020; Sales et al., 2020; Mena et al., 2021; Kim et al., 2022; Mas-Carrió et al., 2022). Comparatively, smaller, more cryptic mammals are generally detected better with eDNA (Harper et al., 2019; Mena et al., 2021; Ryan et al., 2022). However, as previously discussed, sampling substrate can also influence detectability, as ingested DNA derived from flies is well suited to detecting arboreal species (Gogarten et al., 2020; Massey et al., 2022), which are difficult to detect with standard camera trapping methods (Moore et al., 2021).

Obtaining perfect congruence between metabarcoding-based methods and traditional methods is impossible because the character of the data is completely different, and this should not impede the application of eDNA-based tools (Pawlowski et al., 2021). Instead, eDNA metabarcoding should be considered an important addition to the ecological monitoring 'toolkit' and continue to be used to complement more established monitoring techniques within terrestrial contexts. Within the context of rewilding monitoring, if the aim is to consistently monitor a wide scope across the tree of life, a multi-method 'toolkit' sampling design would likely be the best approach. For its wider

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implementation, this 'multi-tool' approach will likely need to be balanced with the relative costs of different methods. eDNA metabarcoding in particular has been shown to be comparatively lower cost to more traditional methods across different contexts (Fediajevaite et al., 2021), though this can vary, particularly for sites with lower taxonomic diversity (Bálint et al., 2018).

Limitations and research gaps

Our meta-analysis is based on studies that display a high degree of heterogeneity in terms of study design, and approach to data collection and analysis. To overcome this caveat requires large-scale individual studies that compare methods in the same way across diverse systems, and the adoption of method standards across studies; something that the global eDNA research community is starting to address (Hirsch et al., 2024).

Questions still remain regarding the best eDNA substrate choice for terrestrial monitoring. Notably, airDNA has not yet been ground-truthed against other survey methods, and there is much to learn about how it compares to other eDNA approaches. Improved understanding of the 'ecology of eDNA' and its persistence in terrestrial settings would also enable a more informed choice of sampling substrate (Leandro et al., 2024). Additionally, despite suggestions that sampling multiple substrates can ensure more comprehensive ecological monitoring (Hassan et al., 2022), only a small proportion of the terrestrial eDNA studies reviewed here did this, and many studies failed to justify their substrate choice or acknowledge alternatives. Improving transparency and reproducibility in metabarcoding workflows is a priority across all studies to facilitate better sampling strategies and uptake of eDNA for terrestrial monitoring.

Questions also remain around the best combination of survey methods to use for the rewilding monitoring toolkit. Our results suggest a multi-method strategy, using a combination of metabarcoding and established survey methods, increases the number of taxa detected. However, comparisons between metabarcoding and acoustic monitoring, which is emerging as a highly effective survey tool in terrestrial settings, were a notable omission from our reviewed papers. Acoustic monitoring has so far only been compared to eDNA in aquatic (Easson et al., 2020; Sato et al., 2021) or species-specific contexts (Takahara et al., 2020), though results indicate similar, patterns to our general findings, with detectability of taxa for either method depending on the ecological characteristics of the respective target species. The level of disturbance created by different methods and how this could impact the nature-driven ethos of rewilding should also be considered. For example, while eDNA sampling can offer a detailed snapshot of a community, sampling may still cause disturbances, and this level of data may only be necessary at key milestones during a project's trajectory. More continuous monitoring methods, such as camera or acoustic tools, may provide sufficient data between surveys, whilst providing additional data regarding population sizes and behavior (O'Connell et al., 2010; Marques et al., 2013). Understanding the efficacy of metabarcoding at different stages during a project's progression may be crucial for its effective integration into rewilding research and practice.

Rewilding aims to restore the functional ecology of ecosystems (Torres et al., 2018) but our review highlights that few terrestrial metabarcoding studies perform functional diversity and/or network analyzes. The assignment of functional groups is possible from DNA data, by using functional trait databases that exist for certain taxonomic groups (e.g. fungi FunTraits, Põlme et al., 2020), though reference database gaps can create uncertainty and bias in functional diversity estimates (Condachou et al., 2023). Ancillary information is often required to associate taxa with functional traits or trophic levels and the availability and reliability of this information may limit the uptake of functional analyzes with DNA metabarcoding data (Evans et al., 2016; Pereira et al., 2023). Trophic networks can be readily constructed, and network parameters estimated via DNA metabarcoding of feces or iDNA, or, from swabs of plants and pollinators (Evans and Kitson, 2020). Networks can also be constructed just from community composition data, by assigning functional feeding groups from literature or databases, but few eDNA studies have yet adopted this approach (but see Blackman et al., 2022) but our review highlights that few terrestrial metabarcoding studies perform functional diversity and/or network analyzes. The assignment of functional groups is possible from DNA data, by using functional trait databases that exist for certain taxonomic groups (e.g. fungi FunTraits, Põlme et al., 2020), though reference database gaps can create uncertainty and bias in functional diversity estimates (Condachou et al., 2023). Ancillary information is often required to associate taxa with functional traits or trophic levels and the availability and reliability of this information may limit the uptake of functional analyzes with DNA metabarcoding data (Evans et al., 2016; Pereira et al., 2023). Trophic networks can be readily constructed, and network parameters estimated via DNA metabarcoding of feces or iDNA, or, from swabs of plants and pollinators (Evans and Kitson, 2020). Networks can also be constructed just from community composition data, by assigning functional feeding groups from literature or databases, but few eDNA studies have yet adopted this approach (but see Blackman et al., 2022).

Metabarcoding of eRNA is gaining traction for biodiversity monitoring because of its greater lability and potential for distinguishing live from dead sources, compared to eDNA (e.g. Cristescu, 2019; Littlefair et al., 2022). eRNA is also arguably more suited than eDNA to studying ecosystem function, as it allows the detection of changes in expression of single or multiple genes or whole metatranscriptomes in response to environmental change (Yates et al., 2021; Hechler et al., 2023). However, eRNA analysis is still in its infancy relative to eDNA metabarcoding, so was not included in our review. Studies that ground-truth eDNA and eRNA analyzes against traditional monitoring in terrestrial contexts would be useful to understand the relative pros and cons of the different approaches.

Finally, it should be noted that although metabarcoding is currently the most widely used approach for community analyzes of eDNA, bulk or iDNA samples, it is not the only molecular approach to biodiversity monitoring, and it has its limitations, particularly in relation to amplification bias during PCR (see e.g. Nichols et al., 2018). Hybridization capture (or target enrichment metabarcoding), which utilizes oligonucleotide baits complementary to barcodes or other regions of interest, for example, is an emerging PCR-free alternative to traditional metabarcoding, but not without its own biases and limitations (Giebner et al., 2020; Nota et al., 2024). These emerging molecular technologies hold promise for the monitoring of rewilding projects, but further research is required to establish their uses and limitations.

Conclusion

Adaptive ecological monitoring plays a pivotal role in understanding ecosystem dynamics and informing management strategies for terrestrial rewilding projects. Although underutilized in terrestrial contexts, eDNA metabarcoding offers promise in striking the balance between minimizing disturbance and maximizing data collection efficacy across different ecosystems and taxa. However, it is imperative that sampling design, substrate(s) and assay choice are carefully considered as these choices are highly context dependent. Monitoring strategies for rewilding need to be designed to encompass spatial and temporal variability of ecosystems and distributions of taxa. A combination of eDNA and other survey methods will maximize taxonomic coverage, but eDNA has a clear role to play as a complementary tool in rewilding and other terrestrial monitoring schemes.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

CC: Conceptualization, Writing – original draft, Writing – review & editing, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization. JG: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing. IC: Conceptualization, Project administration, Supervision, Writing – original draft, Writing – review & editing. LLH: Conceptualization, Funding acquisition, Investigation, Methodology, Project Administration, Supervision, Validation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1473957/full#supplementary-material

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