Downloaded from https://www.pnas.org by UK CENTRE FOR ECOLOGY & HYDROLOGY (CEH) on August 21, 2025 from IP address 192.171.199.129,

Biodiversity conservation requires integration of species-centric and process-based strategies

Joseph A. Tobias^{a,1} , James M. Bullock^b, Lynn V. Dicks^c, Brenna R. Forester^d, and Orly Razgour^e

Edited by Anne Yoder, Duke University, Durham, NC; received August 16, 2024; accepted April 2, 2025

Conservation science and policy are geared primarily toward the preservation of species and habitats, with priority often given to the rarest, most vulnerable or most charismatic forms. This pattern-based approach has broad appeal and offers a pragmatic short-cut for targeting conservation action. However, the long-term efficacy of species and landscape conservation programs remains highly uncertain, amid growing evidence that sustainable conservation action requires an increased emphasis on preserving ecological and evolutionary processes. This reframing of conservation goals was first proposed 50 y ago, but the concept has struggled to gain traction, particularly in terms of translation into policy. Nonetheless, recent events have shifted the narrative, with multiple interlinked global challenges—including biological invasions, food security, disease, and climate change—putting ecological processes firmly back on the agenda. Concurrently, conservation finance is changing rapidly, driven in part by the 2022 Kunming-Montreal Global Biodiversity Framework, which prioritized actions to enhance and restore ecosystem stability, connectivity, and resilience. These ecosystem properties are fundamentally process-driven and appear to create an operational gulf between current conservation practice and the targets of international agreements. We describe how new approaches can be used to close this gap by redirecting conservation attention toward processes at the heart of ecosystem function, including adaptation, gene flow, dispersal, and trophic interactions. Wider adoption of these approaches is urgently needed to forge a deeper connection between conservation practice and policy targets, thereby ensuring that ongoing investment in biodiversity conservation goes beyond damage limitation and instead leaves a lasting legacy of resilient ecosystems.

biodiversity conservation | ecosystem function | resilience | species interactions | sustainability

Aldo Leopold, whose writings helped to catalyze the American environmental movement, once memorably advocated for biodiversity conservation by stating that "to keep every cog and wheel is the first precaution of intelligent tinkering." This conceptualization was ahead of its time: the natural world as a vast metaphorical machine, in which the cogs and wheels are species, interconnected in complex and often uncertain ways, such that the loss of any component part may have unintended consequences for the system as a whole. Leopold's plea for precaution extended to our relationship with land as well as species, yet the species-centric rationale struck the deepest chord in the public consciousness and

the primary goal of biodiversity conservation is still generally assumed to be the prevention of species extinctions (1-6). This goal has proved to be an effective focus for conservation action, although many critiques have pointed out that it prioritizes representation (pattern) over persistence (process), with major implications for the future of biodiversity and ecosystem function (7-11).

In terms of basic species preservation targets, biodiversity conservation has been relatively successful. Many of its core metrics and policy innovations—including the US Endangered Species Act, the International Union for Conservation of Nature (IUCN) Red List (12), the Convention on International Trade in Endangered Species [CITES; (13)], and the Species Threat Abatement and Restoration (STAR) metric (14)—are largely focused on preserving species. Conservation funding has been funneled into biodiversity hotspots based on their species richness and endemism (e.g., ref. 2), and the global protected area network is increasingly designed to avert species extinctions, with major programmes focused on ensuring that all species are represented in at least one protected area worldwide (3, 4, 15). In addition, targeted conservation interventions have kept several Critically Endangered species on life support (16), thereby slowing the rate of extinction (17). These successes are rightly celebrated, but are they sustainable?

A fundamental problem is that many current conservation strategies are geared toward saving the rarest or most charismatic species, many of which end up surviving in small in-situ or ex-situ populations sustained by protected areas and captive breeding programmes. Moreover, targeted interventions are relatively sparse or ineffective, even for birds and mammals, only ramping up when species are under extreme threat of extinction (6, 16). Taking this strategy to its logical conclusion, the likely endgame is a "Noah's Ark"

Author affiliations: ^aDepartment of Life Sciences, Imperial College London, Ascot SL5 7PY, United Kingdom; ^bUK Centre for Ecology & Hydrology, Wallingford OX10 8BB, United Kingdom; Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, United Kingdom; dUnited States Fish and Wildlife Service, Fort Collins, CO 80525; and eBiosciences, University of Exeter, Exeter EX4 4PS, United Kingdom

Author contributions: J.A.T. designed research; and J.A.T., J.M.B., L.V.D., B.R.F., and O.R. wrote the paper.

Competing interest statement: LVD is a Non-Executive Director of Natural England, the UK Government's statutory nature conservation adviser for England. The other authors declare no competing interests.

Copyright @ 2025 the Author(s). Published by PNAS. This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-

¹To whom correspondence may be addressed. Email: j.tobias@imperial.ac.uk.

This article contains supporting information online at https://www.pnas.org/lookup/ suppl/doi:10.1073/pnas.2410936122/-/DCSupplemental.

Published July 28, 2025.

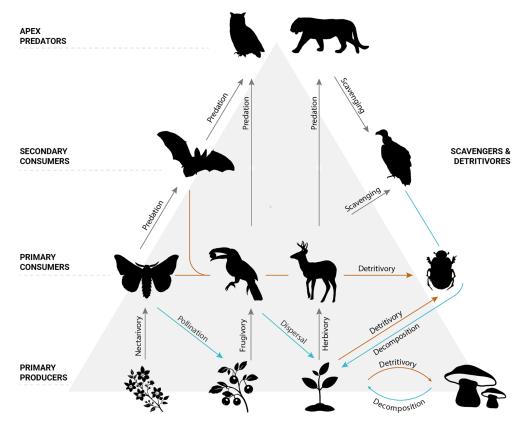


Fig. 1. Most conservation initiatives are species-centric, focusing on preserving representation (pattern) rather than persistence (process). Species-centric strategies are mainly geared toward avoiding extinction, often prioritizing rare or charismatic species, but ignoring ecological roles and interactions. To illustrate how process-based conservation differs from the current paradigm, this diagram shows a simplified ecological network, represented as a trophic pyramid. In this schema, the sun's energy is taken up by primary producers (plants), after which it flows through the biosphere via trophic processes (gray arrows) regulated by consumers and scavengers (animals). These processes are accompanied by additional feedbacks between trophic levels (blue arrows). Plant-nectarivore interactions drive pollination, leading to plant-frugivore interactions which in turn drive seed dispersal. Germination of seeds then leads to plant growth and plant consumption by herbivores. The flow of energy and nutrients to higher trophic levels is recycled by detritivores (brown arrows), and decomposers, including microbes. The integrity and resilience of ecosystems depends on the abundance and diversity of organisms participating in these trophic interactions, along with a wider range of evolutionary and assemblage-level processes, including adaptation, gene flow, dispersal, and host-pathogen dynamics (*SI Appendix*, Table S1). Sustainable conservation of ecosystems requires an integrated approach that extends beyond species conservation and prioritizes the restoration and management of ecoevolutionary processes. Credits for images from PhyloPic: T. Michael Keesey (owl, flowering plant, seedling plant); Andy Wilson (tiger, deer); Yan Wong (bat); Kaija Gahm (vulture, licensed under CC BY 4.0); German Martínez-Redondo (moth); Gabriela Palomo-Munoz (toucan, licensed under CC BY 4.0); Kristina Gagalova (beetle, licensed under CC BY 3.0); Mason McNair (fruiting plant); Carlo De Rito (mushroom).

scenario in which many species are preserved in tiny or isolated populations, contributing little if anything to ecological processes, having disappeared from most of their historical distribution (10).

Over the last 50 y, nature has been in full retreat. Human actions have caused at least a halving, and perhaps even a ~70% decline, in the global population of wild animals since 1970 (18), including the near-total collapse of many vertebrate populations on land (19) and in the world's oceans (20). The astonishing pace of these declines is driven by a barrage of threats—including habitat loss, overexploitation, pollution, invasive species, and climate change—which have intensified almost unchecked throughout this period (6, 21, 22). From the standpoint of preserving intact and functional ecosystems, therefore, conservation appears to be failing spectacularly.

The ongoing rapid decline in biodiversity has raised questions about whether conservation strategies are fit for purpose, particularly in this era of accelerated global change (11, 23). Saving small and fragmented populations of species is a doomed strategy because it overlooks the complex web of interactions and processes that make ecosystems work (Fig. 1). Moreover, if the organisms participating in this

network need to adapt or disperse in response to changing environmental conditions, then a radical rethink is required (10, 24, 25). As biodiversity recedes into zoos, botanic gardens, and dwindling pockets of protected habitat, key evolutionary and ecological processes are being disrupted at a global scale, with major implications for the long-term stability, adaptability, and resilience of ecosystems. Mass extinction may have been temporarily averted (16, 17), but functional extinction has not (26).

Evolutionary biologists and ecologists have repeatedly called for a more holistic approach to biodiversity conservation, dialling down the traditional focus on species or habitats, and instead emphasizing ecological and evolutionary processes (7, 10, 27) (Fig. 2). We briefly outline the history of this proposal and examine the reasons why it has taken so long to permeate into national and international policy frameworks. We then set out a proposal to implement a process-based conservation strategy for the world's ecosystems. To accelerate this transition, we provide a preliminary roadmap for science and policy, including a summary of recent technical advances and suggested avenues for further research and innovation.

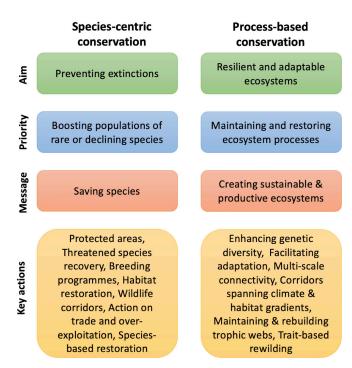


Fig. 2. Summary of distinctions between species-centric and process-based approaches to biodiversity conservation. Conservation science and policy tend to emphasize the preservation of rare species, widely viewed as the primary goal of conservation. Critics of this approach suggest that it will lead to long-term declines in biodiversity and ecosystem function without increased emphasis on process-based conservation. Note that actions listed under process-based conservation are complementary to species-centric approaches; for example, "Enhancing genetic diversity" and "Facilitating adaptation" have already been integrated into species-based conservation actions under the US Endangered Species Act. Rather than favoring one approach over the other, we advocate that efforts to protect and enhance evolutionary and ecological processes should be further integrated into species-centric approaches. Examples of key actions are chosen to highlight distinctions and are not intended to provide a comprehensive assessment. See SI Appendix, Table S1 for further details.

How to Save the Sinking Ark

The idea of redirecting conservation attention to processes generating and sustaining biodiversity was first proposed half a century ago (27). In its original form, the concept focused on maintaining genetic diversity to promote adaptation and resilience. Two decades later, Smith et al. (7) expanded the proposal to include a wider array of evolutionary and ecological factors, including pollination and seed dispersal, describing such processes as "the missing element of conservation programs." Another three decades then passed with relatively little progress in terms of translating these ideas into institutional or governmental policy. Why?

The main reason for this inertia appears to be the cultural and operational challenge of implementing a more holistic approach. The widespread adoption of a process-based strategy would require structural and systemic change, which in turn requires advocacy and effort. It is difficult to make these changes when so much of conservation theory, policy, and legislation is built around the concept of saving threatened species. Even now, the text of the 2022 Kunming-Montreal Global Biodiversity Framework (GBF)—a strategic plan adopted by 196 countries to implement the Convention on Biological Diversity (CBD)—tends to be analyzed from a species-conservation perspective (28). As with any cultural

shift, the initial step is to achieve a consensus around the need for transformative change, requiring integration and communication across different research and policy cultures. Currently, scientists advocating for a transition to processbased conservation still face blank stares from policymakers and opposition from conservation professionals reluctant to abandon a well-oiled modus operandi. There is seemingly an unbridged divide between one faction that believes focusing on processes rather than species is not really conservation, just an offshoot of ecology, and another faction convinced that process-based conservation is the only viable method of saving species over longer timescales (9, 10).

We see evidence of this divide in divergent approaches to biodiversity indicators. The search for actionable targets in a form digestible to business and governments has led to proposals for simplified biodiversity metrics based on either rates (5) or probabilities (29) of species extinction. This is Leopold's cogs-and-wheels analogy reimagined in metric form: everything reduced to minimizing the numbers of species discarded while we meddle with ecosystems. Extinctionbased metrics have some validity under a species conservation paradigm, but conflict with process-based conservation for several reasons (30). First, extinction is not easy to confirm or predict, as the tale of the ill-fated Ivory-billed Woodpecker attests (31). Second, such methods are mainly relevant to charismatic macrofauna and tend to ignore a wide spectrum of biodiversity with crucial functions, including invertebrates, plants, and microbes, where species are poorly known or arbitrary (30). Third, an emphasis on species survival regardless of context promotes a reactive "fire-fighting" approach, leading to costly management of rare species in small and isolated populations. Ultimately, while the goal of zero extinction is laudable and comforting (3), it falls short of ensuring either the long-term viability of species populations or sustainability of ecosystem function, which is only weakly connected to species richness (32, 33).

A range of alternative biodiversity indices can claim to provide indirect measures of ecosystem processes. For example, the Living Planet Index (34) and Essential Biodiversity Variables (35) include estimates of species abundance or population density, providing a metric for the amount of diversity able to deliver ecological functions, at least for better-known vertebrates. Similarly, the IUCN Green Status of Species attempts to evaluate species not against level of threat, but according to their level of recovery toward an estimated baseline of abundance and functionality (36). These approaches may offer deeper insights than extinction-based metrics, and provide more ambitious conservation targets than simply avoiding species extinction. However, each has multiple limitations, including uncertain correlation with ecosystem processes, weakly defined or potentially invalid baselines, and inherent biases (e.g., ref. 37).

Another subset of metrics—including phylogenetic diversity (PD) and functional diversity (FD)—were developed to provide insight into the functional richness and conservation value of biodiversity, based on the assumption that higher levels of PD and FD are correlated with the variety of ecological roles within species assemblages (38, 39). Put another way, PD and FD are standard methods for estimating "portfolio effects" relating to the feature diversity of a given system, with a diverse "portfolio" of features tending to confer stability (40, 41). Used in combination, they are likely to capture more information about resilience and stability than species lists alone (42). These metrics have been influential within the research community, but they are generally seen as too complex for adoption by government agencies or corporations, while at the same time barely scratching the surface in terms of capturing key ecological processes (43, 44).

Set against this backdrop of divided opinion and unresolved metrics, international support for process-based thinking in conservation policy has recently surged. This change in stance is reflected in the GBF text adopted in 2022. The final version continues to highlight species conservation, including an ambitious target to halt human-caused extinctions of native wild species by 2030. Crucially, however, species-centric targets are now accompanied with explicit goals of maintaining, enhancing, and restoring the integrity, connectivity, and resilience of all ecosystems. The concept of ecosystem integrity is well established in environmental policy but hard to define. It refers to ecosystem intactness, meaning the degree to which ecosystems are complete, functional, and similar to their natural state (45).

The increased emphasis on process-based concepts has major implications for governmental agencies and corporate management, who now look to academia and conservation organizations to provide methods for setting and measuring progress toward these objectives. Unfortunately, the collective response is often a range of conflicting opinions about how to define and measure the relevant properties of ecosystems (46, 47), and an assortment of metrics with limited relevance to process-based conservation because they have been designed according to species-conservation principles (e.g., ref. 14 and 48). Ongoing uncertainty about the best metric or metric set for international and corporate policy is slowing down conservation action. In the following sections, we examine three interconnected themes holding the greatest promise for building consensus and accelerating progress toward a more holistic conservation strategy.

Evolution

Previous applications of process-based perspectives to conservation have mainly focused on genetic approaches (10, 27, 49, 50), often inspired by the study of genetic diversity and gene flow across suture zones (9). Genetic variation within populations provides the raw material for evolution and thus reflects the evolutionary potential of species. According to this view, conservation should seek to manage genetic diversity among populations within a species to improve chances for evolutionary adaptation to new challenges such as disease, habitat alteration, and climate change. Growing concern about these threats has accentuated recent interest in the practical applications of conservation genetics (51, 52). Indeed, the conservation of genetic diversity in wild species is perhaps the best example of how process-based thinking can feed directly and harmoniously into species-centric conservation strategies since the idea is now embedded in multiple national and international policy mechanisms, and implemented through species recovery programs (50, 53, 54).

Initial progress in this field involved harnessing data from molecular analyses to identify reciprocally monophyletic lineages—so-called Evolutionarily Significant Units (ESUs)—as a way of prioritizing the conservation of intraspecific genetic diversity (55). It is often unclear which intraspecific lineages are best-adapted to future environmental conditions, suggesting that "bet-hedging" is required, with conservation resources shared among ESUs rather than concentrated in a single lineage. Diagnostic or diverging intraspecific lineages can also be conceptualized as incipient species; that is, lineages undergoing the process of speciation and which deserve protection as "future species" (9). The distinction between ESUs and species is often fuzzy, with small but consistent genetic divergence regularly used to propose that intraspecific lineages are independent species, a common practice in high-profile taxa such as primates (e.g., ref. 56). Given the relevance of taxonomic species units to conservation funding and legislation, the decision about whether these lineages should qualify as species is often contentious for standard conservation programs (57, 58). The question is less thorny for process-based thinking as all intraspecific lineages are deemed worthy of conservation.

Early definitions of ESUs based around reciprocal monophyly have been largely discarded as overly simplistic (59) and replaced by alternative methods. With advances in high-throughput sequencing, ESUs can now be delineated for conservation by incorporating neutral and adaptive variation to estimate whether genetic differences reflect adaptation—that is, differentiation by selection (60, 61). The concept of ESUs can also be expanded to identify evolutionary hotspots of phylogenetic uniqueness or high rates of evolutionary change, which can differ from hotspots defined by species richness or protected area networks (62). Actions targeted at maintaining evolutionary hotspots may help to conserve biodiversity over longer timeframes.

Development and testing of methods for adoption by the CBD suggest that genetic indicators can serve as proxies for genetic diversity when data are available (54), prompting calls to include metrics of genetic diversity in Red List assessments (52). In general, conservation efforts should maintain large, connected populations to prevent the loss of genetic diversity and to boost adaptive capacity (51). However, the goals of process-based conservation are not always met by maximizing genetic variation. In some cases, it can be important to maintain locally adapted populations and avoid swamping the local genome through introgression (63). Efforts to increase connectivity should not seek to establish dispersal and gene flow across barriers that have existed over an evolutionary time scale, but rather across more recent, anthropogenic barriers.

Movement

Patterns of gene flow, population genetic structure, and the degree of molecular divergence among evolutionary lineages are all closely related to the movement of individual organisms (64). Animal movement also underpins a range of ecological processes influencing species survival, with effects that cascade through trophic levels. For example, many plants rely so heavily on dispersive animals as "mobile links" to transfer pollen and seeds across the landscape that their

populations collapse when pollinators or seed dispersers are removed (65-67). Accordingly, human impacts on populations of large seed-dispersing animals have serious implications in the era of climate change because defaunation and land-use change leave plants less able to track their climate niches (68, 69). Through a variety of mechanisms, dispersal is a key factor determining species responses to stressors, including habitat fragmentation (70) and climate change (71). Understanding not just species differences in dispersal abilities and mechanisms, but also how landscape features can hinder or facilitate dispersal, are therefore vitally important for conservation (72, 73).

Standard approaches to species conservation have struggled to deal with the current and likely future movement of biodiversity. Protected areas form an inherently static and patchy mosaic distributed across an increasingly inhospitable matrix, often precluding movement of individuals between isolated fragments of natural habitat (73). The problem is exacerbated by climate change, which is driving widespread shifts in geographical distribution (25, 74). Previously, range shift projection models under different climate scenarios assumed that species populations disappearing from one protected area would reappear at another area within the expected future distribution of their climatic niche (e.g., ref. 75). In reality, any projected turnover of vulnerable species from one protected area to another will be highly achievable for mobile or dispersive species but unlikely for habitat specialists with poor dispersal ability, since in these cases the intervening matrix between reserves is impermeable. More recent range-shift models incorporate estimates of landscape permeability (e.g., refs. 76 and 77), although attempts to include differences in species dispersal ability remain preliminary.

Another substantial shift toward process-based thinking is evident in spatial conservation planning (68). It is now widely acknowledged that strategies supporting metapopulation or metacommunity dynamics, such as establishing and protecting dispersal corridors, or otherwise increasing the permeability of landscapes outside protected areas, are vital for maintaining gene flow and sustaining ecological processes (73, 78, 79). A coherent global strategy for achieving ecological connectivity is needed, including efforts to measure and monitor the effectiveness of connectivityboosting policies in different ecological contexts. In general, corridor conservation programs need to be scaled up more ambitiously, along the lines of the Yellowstone to Yukon Conservation Initiative, a transboundary effort restoring landscape connectivity across a vast North American region (79). Similar programs are required worldwide, particularly in tropical forests, where a large proportion of native species are highly vulnerable to habitat fragmentation (70, 80). Another priority—often proposed, but rarely achieved—is to establish connectivity corridors aligned with habitat and climate gradients, including elevational gradients, to allow species assemblages to track fluctuating environmental conditions over longer timeframes (7, 81, 82).

Long-distance migration is a special case of animal movement that poses particular problems for conservation. Many vertebrates and invertebrates, in both terrestrial and marine realms, undergo seasonal journeys to evade harsh conditions or to track food and other resources (83). Uneven patterns

of climate change around the globe are lengthening or impeding many of these migrations, placing pressure on migratory species (84). Furthermore, migrants often pass through many different countries, such that highly localized threats can drive population declines, overriding conservation actions in other parts of the range. Overcoming these problems is a high priority, not least because animal migrations provide flexible responses to climate change through seed dispersal (85) and play crucial roles in other vital processes and services (86). For example, many native pollinators have been removed from the British countryside by habitat loss and pollutants, but negative environmental impacts are currently offset by billions of hoverflies that visit Britain as seasonal migrants from less-intensively developed regions of Europe, importing vital services of pollination and pest control (87).

The conservation of migrants can only be achieved with a massive-scale, process-based strategy, including flyway management schemes based on international and intercontinental agreements. Given that migratory species tend to "fan out" and disperse widely during the nonbreeding season, management of their populations cannot rely exclusively on site-based protection, and instead must prioritize "shallow" actions, providing wildlife friendly habitats across extensive areas (88). In many cases, it is also vital to implement siteand landscape-level conservation situated between the breeding and nonbreeding ranges, to provide safe refuge and efficient stop-overs during migratory journeys (84). Animal movement in general, and migration in particular, highlight the urgent need to adopt dynamic and flexible conservation strategies focused on preserving and enhancing dispersive processes (89).

Interactions

Species interactions are fundamental to ecological processes and associated ecosystem services (90). In particular, trophic interactions regulate the flow of energy and nutrients between trophic levels, influencing the stability and resilience of ecosystems (Fig. 1). Yet standard conservation programmes rarely target interactions or use the health of interactions as the metric for determining the success of interventions.

Two classic examples of stabilizing interactions are nectarivory and frugivory, the primary driving forces behind pollination and seed dispersal, respectively. Almost 90% of the world's flowering plant species are animal-pollinated (91) and over half of global plant diversity requires animals for seed dispersal, a proportion rising to 70 to 90% in the tropics (92). Declines in the distribution and density of animal populations can therefore reduce pollination rates, fruit set and seed dispersal across much of the historical range of plant species (66, 67, 93-95). Lower recruitment in food plants will in turn limit the supply of food available to higher trophic levels. Ultimately, these negative feedbacks are likely to constrain important attributes of ecosystems, including primary productivity, carbon cycling, and, in some cases, agricultural crop production (96).

The diversity, distribution, and abundance of species at all trophic levels are strongly mediated by a wider set of biotic interactions with ecological competitors, predators, herbivores, parasites, and pathogens. Predators of vertebrate and invertebrate animals play critical roles in controlling prey populations, strongly influencing vegetation dynamics and nutrient cycling. The removal of apex predators, such as wolves or sharks, can lead to trophic cascades, where the absence of top-down control results in overpopulation of herbivores and subsequent overgrazing (97). Ultimately, this can cause habitat degradation and loss of biodiversity in terrestrial and marine systems alike. Similar negative outcomes occur in landscapes with depleted assemblages of insectivores, since phytophagous insects can proliferate, constraining productivity, and damaging crops. Finally, detritivores and scavengers play important roles in stabilizing ecosystems by regulating waste disposal and energy flows between trophic levels.

Rather than solely preventing extinctions or maintaining a network of protected areas, conservation should redirect action and policy directives toward designing and managing landscapes for the enhancement of species interactions, trophic processes, and nutrient cycling (*SI Appendix*, Table S1). Management strategies can be explicitly designed to promote mutualistic interactions, such as pollination and seed dispersal (98), which are key to the movement of genetic material across the landscape, as well as to natural processes of habitat recovery and restoration (99, 100). Equally, attention should focus on maintaining populations of scavengers, as well as antagonistic species interactions—such as competition and predation—where these function in stabilizing and diversifying ecosystems.

In many cases, interactions resulting in interspecific competition, parasitism, or disease may seem to fit poorly into a conservation strategy. Nonetheless, we cannot hope to understand the impacts of global change on future ecosystems without understanding species interactions, and accounting for them in predictive models (101-103). The movement of species around the planet by humans, and in response to climate or land-use change, is bringing together novel communities with uncertain interactions among species. For example, exploitation competition and interference competition can result in competitive exclusion or divergent selection (character displacement) while hybridization can lead to reproductive interference or genetic introgression (104). All these factors shape how organisms adapt to environmental change (105) and determine whether species are likely to coexist (102). Advances in evolutionary biology and trait-based ecology mean that we are now equipped with the tools to understand and predict these outcomes with greater certainty.

Risks, Imperatives, and Operational Challenges

The economic imperative of managing sustainable ecosystems brings to mind the financial benefits of an effective global program for biodiversity conservation highlighted by Balmford et al. (106). We suspect that species-centric conservation entails much higher financial risk because targeted actions to prevent extinctions are expensive (107), and more species will become threatened over time if they inhabit unsustainable ecosystems. Furthermore, a strategy

prioritizing the conservation of rare species may work in the short term, but could ultimately fail if ecosystems malfunction or collapse.

Integrating species-centric with process-based approaches will require transformative change and an initial phase of financial investment. The emphasis shifts toward regional, landscape-level, and transboundary conservation initiatives that are often politically and financially complex, requiring investment into the underlying administrative structures and policy mechanisms that make them work. Attention should focus on navigating trade-offs when process-based approaches conflict with standard targets of species-centric approaches (Fig. 2). For example, is it acceptable to promote ecosystem function and stability by introducing nonnative species? Should we allocate scarce resources to promoting FD and bioabundance rather than saving the last remnants of a dwindling species? And do we allow the modification of these rare and declining forms through hybridization with successful relatives, on the grounds that ecologically important populations may then be better adapted to changing conditions (108)? While these potential conflicts need to be acknowledged and managed, the species-centric and process-based elements of a unified conservation strategy can work in synergy, particularly over longer timescales. For example, a process-based approach maintaining the functional integrity and diversity of a given ecosystem can result in the alleviation of threats to individual species (109).

Progress and Policies

It has taken half a century since Frankel (27) argued that the long-term future of biodiversity depended on safeguarding processes rather than species for a process-centric conservation ethic to finally permeate into financial directives and international agreements. The revised GBF text adopted in 2022 suggests a new era is beginning, with ecosystem integrity and resilience repositioned to center stage. Fundamental shifts in the regulatory landscape and associated mechanisms, such as the Taskforce on Nature-related Financial Disclosures, are changing the way governments and corporations report on their nature-related risks and actions, with the aim of funneling global financial flows toward naturepositive outcomes. In conjunction, many conservationists are recognizing the need to move away from the traditional focus of attempting to preserve ecosystems as they once were, toward actions that facilitate their adaptation and transformation in response to change (10, 11, 23, 110). We now face the problem that there seems to be little agreement about how to achieve these goals.

New environmental policies are being devised in a range of contexts from international agencies to local councils, often with the target of restoring ecosystem processes. However, measuring the success of such policies remains challenging. What outcome metrics should we use, and how do we know which metric works best at particular spatial and temporal scales? The following sections outline key opportunities for incorporating ecological and evolutionary processes into biodiversity conservation and policy, highlighting themes in need of research and innovation.

Genetic Analyses

Since the 19th century, wildlife populations have undergone a substantial erosion of genetic variation (111), often attributable to habitat loss, overexploitation (112), or climate change (113). In theory, genomic data can be used to estimate the vulnerability of populations to future environmental change by identifying mismatches between contemporary and predicted future genotype-environment relationships (114). For example, Razgour et al. (115) developed a genome-informed framework to assess population vulnerability to climate change based on the estimated level of exposure to future changes, likely sensitivity to those changes, and range shift potential (inferred from the effect of landscape barriers on gene flow). Adaptive genetic variation can also be directly integrated into species distribution models [genomic-informed SDMs: (116)] and individual-based ecoevolutionary models (e.g., refs. 117 and 118). These approaches offer some promise as methods for predicting future range shifts or the scale of gene flow from populations better-adapted to future climatic conditions (evolutionary rescue). However, such applications remain exploratory and require validation by further research.

The maintenance of genetic variation is now highlighted as a goal of global conservation policy in the GBF, driving wider monitoring of genetic variation over space and time through large-scale sequencing missions [macrogenetics; (119, 120)]. These initiatives are opening up the potential for gene-focused Essential Biodiversity Variables (54, 121), along with regional-scale programs estimating genetic variation and connectivity (e.g., ref. 122). Genetic data at this scale can be used in multispecies, ecosystem-level conservation planning, with an emphasis on preserving and enhancing adaptive capacity and connectivity (121), although the links between genetic data and ecosystem integrity or resilience remain challenging to quantify. In addition, costs are prohibitive and the patchy availability of genetic data remains a serious issue (123), particularly in underresourced, megadiverse countries. Brazil, for example, has access to genetic studies of <0.5% of its ~60,000 native plant and vertebrate species (124). Further validation and development of genetic indicators is a priority, coupled with the expansion of sequencing efforts where feasible.

Interventions to Boost Ecological Processes. Local-scale studies have demonstrated that important processes can be accentuated by landscape management practices. For example, minor habitat adjustments at the farm-field scale can boost bee populations with benefits for crop pollination (125) while seed dispersal can be boosted by creating patches of natural vegetation in landscapes earmarked for restoration, e.g., applied nucleation (126). At a wider scale, the application of metapopulation theory has driven progress in spatial modeling techniques to quantify connectivity across landscapes and between protected areas (e.g., refs. 127-129). The next phase of process-based conservation should focus on developing and applying these methods to identify priority areas for landscape management, including sites that require protection or restoration to improve connectivity. A wide selection of connectivity enhancement interventions can work in different contexts, including corridors, stepping stones, or other methods to improve permeability of the matrix (73). Further research is needed into the design of

connectivity interventions, including conservation action plans for migration corridors and flyways.

Process-based approaches can help to switch focus from charismatic fauna to less-prominent groups that are generally overlooked in species-centric conservation strategies. For example, the current reactive conservation paradigm tends to overlook decomposers and scavengers, despite their vital role in waste disposal and energy flows (130). Asian vultures were largely ignored by conservationists until they had undergone spectacular declines, leading to a collapse in natural waste disposal processes and billions of dollars lost in healthcare costs for India alone (131). A new proactive conservation strategy is required that supports energy flows and nutrient cycles before they collapse through actions that promote diversity and abundance across trophic levels (132), including scavengers and detritivores (130, 133, 134).

Given that so much of wild nature is already highly degraded, much attention has focused on restoring habitats and species assemblages. These efforts are often focused on species representation based on target species lists or priority species, usually with the goal of replacing species lost from a particular environment. However, there is increasing interest in other approaches that move from species targets toward a more functional objective, such as restoring functional complexity (41). The question of whether restoration targets should be simplified to maximizing the functional complexity of habitats and species assemblages or tailored to local contexts using realistic historical baselines and spacefor-time benchmarks (i.e., comparing with more pristine sites nearby and accounting for local environmental conditions) is an important topic for further research (135).

Trophic rewilding is a different procedure which generally focuses on top-down processes by reintroducing apex consumers. The emphasis is usually on restoring lost interactions between animals and plants, thereby returning to a more natural state of ecosystem functioning and dynamics (136, 137). A core debate in rewilding science is whether nonnative megafauna could or should be introduced as ecological surrogates of extinct species or missing functions (138). Evidence suggests that this can work (139) but the procedure is controversial. For example, plans to reintroduce the European bison Bison bonasus to Spain as an ecological analogue of the extinct steppe bison Bison priscus have met with firm opposition (140). Further research is needed to explore best practices in restoration and rewilding, including mixed strategies capitalizing on their different strengths (141). In addition, while rewilding is a viable last-resort, more attention is needed on managing existing biodiversity to enhance resilience; for example, maintaining assemblages of seeddispersing animals can boost natural (and cost-effective) reforestation with native trees and shrubs (99, 100).

Ecosystem Monitoring and Metrics. Most metrics developed to set and track progress toward conservation targets (e.g., refs. 14, 35, and 48) remain explicitly species-centric or have limited connection to ecosystem processes. Those that attempt to consider processes appear to be relatively subjective and limited by data availability. For example, criterion D of the IUCN Red List for Ecosystems focuses on biotic processes and interactions, but this is generally viewed through the lens of abundance or biomass of very few keystone species or, less often, particular functional groups.

Other quantitative metrics that attempt to capture information about species traits include PD and FD, both of which can claim to offer insights as ecosystem metrics (38). PD is correlated with feature diversity, which in turn reflects the number of ecological roles undertaken by a species assemblage, providing a crude metric of ecological functions (142). As pointed out in recent critiques (e.g., ref. 44), the usual approach to PD and FD involves relatively simplistic calculation of diversity across an assemblage or region, with little evidence that this connects to measurable ecosystem functions. However, more targeted applications are possible in better-known groups, such as birds (143). Further research is needed to develop and validate more refined metrics integrating PD and FD (31) and focusing on particular target functions (96). In future, to provide a more explicit connection with ecological processes, these metrics could be combined with other systems, including STAR (14), Key Biodiversity Areas and the Red List of Ecosystems (44).

With the rapid expansion of trait datasets, functional traits provide one of the most promising frameworks for quantifying the integrity and resilience of ecosystems (143), particularly given widespread trait-matching between interacting species, such as correlations between the beak size of frugivorous birds and the fruit size of their food plants (144). Ecological and morphological traits reflect the trophic structure of species assemblages (145), highlighting the integrity of species interaction networks (99, 100), and offering metrics that can outperform species identity in predicting ecosystem function (42, 139, 146). Trait-based metrics can be used to estimate and predict the functional impacts of species loss (147), climate change (148, 149), land-use change (70), and rewilding strategies. However, datasets for most groups remain patchy and metrics of ecosystem function and connectivity remain under construction.

More immediately feasible are approaches based on remote sensing or tracking technology. Data extracted from satellite imagery may provide a short-cut for rapid monitoring of processes (150) and quantifying ecosystem integrity (e.g., ref. 46). However, while such data can provide simple metrics of habitat intactness and connectivity, it likely requires integration with in-situ monitoring of vegetation structure, species assemblages, and trait diversity to provide real insights into the integrity and resilience of ecological processes (151). Ultimately, we need to abandon the search for a single index or method for guiding conservation action and instead develop a toolkit of complementary indices designed for use in different contexts.

Conclusions

In his analogy of ecosystems as complex machines with interacting parts, Aldo Leopold advocated preserving the entire system intact with no part discarded. Conservationists have generally interpreted the parts of ecosystems most worthy of saving as species. However, this misses the point that the essential cogs and wheels sustaining the biosphere are adaptation, movement, and interaction—in other words, not patterns but processes. We need a new analogy for conservation because ecosystems are not mechanical, they are dynamic, ever-changing, and unpredictable systems with emergent properties, more like economies or financial markets. Economists do not generally advocate saving a particular product, or brand, or company. They focus on managing and facilitating processes of supply, demand, productivity, and innovation, much like we are advocating.

We are, of course, not proposing that species are irrelevant or disposable, particularly as they can take millions of years to evolve. Species-centric conservation policies are deeply entrenched and remain vital tools for biodiversity conservation. However, they may be limited in their potential to deliver high-integrity, future-proof ecosystems unless they embrace process-based perspectives [Fig. 2; (7, 10, 44)]. There is an urgent need to integrate a complementary strategy prioritizing the conservation of genetic diversity, adaptive capacity, movement, migration, and critical species interactions, all of which enhance the resilience and adaptability of ecosystems in the face of environmental change. This transformative shift toward process-based thinking appears to be gathering momentum, adding a grander scope to the conservation mission.

The prevention of species extinctions and the restoration of locally extirpated forms back into their previous geographical ranges are, in essence, reactive strategies that seek to maintain ecosystems in an assumed historical state. We advocate a more proactive strategy focusing on protecting and restoring the processes which allow ecosystems to function and adapt to changing conditions (8, 9). Adoption of this framework would ensure that conservation is no longer about preserving the past but also preparing for the future (11, 27). Based on the tone of recent international agreements, the political tide is turning toward this renewed conservation ethic. We advocate integration and communication across the two primary cultures of conservation—species-centric and process-based—as the most effective progress will occur when these two missions operate in tandem and synergistically. Now is the time to reconfigure conservation planning, policy, and practice around a longer-term vision for biodiversity and ecosystems.

Data, Materials, and Software Availability. There are no data underlying this work.

- I. J. A. McNeely, K. Miller, R. A. Mittermeier, W. V. Reid, T. B. Werner, Conserving the World's Biological Diversity (IUCN, 1990).
- 2. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. da Fonseca, J. Kent, Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
- T. H. Ricketts et al., Pinpointing and preventing imminent extinctions. Proc. Natl. Acad. Sci. U.S.A. 102, 18497–18501 (2005).
- 4. A. S. L. Rodrigues et al., Effectiveness of the global protected area network in representing species diversity. Nature 428, 640-643 (2004).
- 5. M. D. A. Rounsevell et al., A biodiversity target based on species extinctions. Science 368, 1193–1195 (2020).
- R. A. Senior et al., Global shortfalls in documented actions to conserve biodiversity. Nature 630, 387–391 (2024).
- T. B. Smith, M. W. Bruford, R. K. Wayne, The preservation of process: The missing element of conservation programs. *Biodiv. Lett.* **1**, 164–167 (1993).
- A. G. Balmford, G. M. Mace, J. R. Ginsberg, "The challenges to conservation in a changing world: Putting processes on the map" in Conservation in a Changing World, G. M. Mace, A. Balmford, J. R. Ginsberg, Eds. (Cambridge University Press, 1998), pp. 1–28.
- 9. C. Moritz, Strategies to protect biological diversity and the evolutionary processes that sustain it. Syst. Biol. **51**, 238–254 (2002).
- D. L. Santamaría, P. F. Méndez, Evolution in biodiversity policy–Current gaps and future needs. Evol. Appl. 5, 202–218 (2012).
- 11. C. J. Gardner, J. M. Bullock, In the climate emergency, conservation must become survival ecology. Front. Conserv. Sci. 2, 659912 (2021).
- 2. G. M. Mace et al., Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv. Biol. 22, 1424–1442 (2008).

- M. Harfoot et al., Unveiling the patterns and trends in 40 years of global trade in CITES-listed wildlife. Biol. Conserv. 223, 47–57 (2018).
- L. Mair et al., A metric for spatially explicit contributions to science-based species targets. Nat. Ecol. Evol. 5, 836-844 (2021).
- S. Le Saout et al., Protected areas and effective biodiversity conservation. Science 342, 803-805 (2013).
- F. C. Bolam et al., How many bird and mammal extinctions has recent conservation action prevented? Conserv. Lett. 14, e12762 (2021).
- M. Hoffmann et al., The impact of conservation on the status of the world's vertebrates. Science 330, 1503-1509 (2010).
- WWF, Living Planet Report 2022–Building a Nature-Positive Society, R. E. A. Almond, M. Grooten, D. Juffe Bignoli, T. Petersen, Eds. (WWF, 2022) L. Greenspoon et al., The global biomass of wild mammals. Proc. Natl. Acad. Sci. U.S.A. 120, e2204892120 (2023).

- L. Greenspoon et al., The global biomass of wild mammals. *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2204892120 (2023).

 D. J. McCauley et al., Marine defaunation: Animal loss in the global ocean. *Science* **347**, 1255641 (2015).

 K. Winkler, R. Fuchs, M. Rounsevell, M. Herold, Global land use changes are four times greater than previously estimated. *Nat. Commun.* **12**, 2501 (2021).

 H. Seebens et al., Projecting the continental accumulation of alien species through to 2050. *Glob. Change Biol.* **27**, 970–982 (2021).

 T. H. Oliver et al., Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* **30**, 673–684 (2015).

 Y. Malhi et al., Climate change and ecosystems: Threats, opportunities and solutions. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **375**, 20190104 (2020).

 B. R. Scheffers et al., The broad footprint of climate change from genes to biomes to people. *Science* **354**, aaf7671 (2016).

 T. Säterberg, S. Sellman, B. Ebenman, High frequency of functional extinctions in ecological networks. *Nature* **499**, 468–470 (2013).

 O. H. Frankel. Genetic conservation: Our evolutionary responsibility. *Genetics* **78**, 53–65 (1974).

- O. H. Frankel, Genetic conservation: Our evolutionary responsibility. Genetics 78, 53-65 (1974).
- P. J. K. McGowan et al., Understanding and achieving species elements in the Kunming-Montreal Global Biodiversity Framework. Bioscience 74, 614-623 (2024).
- A. Eyres et al., Life: A metric for mapping the impact of land-cover change on global extinctions. Philos. Trans. R. Soc. Lond. B Biol. Sci. 380, 20230327 (2025). A. C. Hughes, H. Qiao, M. C. Orr, Extinction targets are not SMART (Specific, Measurable, Ambitious, Realistic, and Time Bound). Bioscience 71, 115–118 (2020)
- J. A. Jackson, Ivory-billed woodpecker (Campephilus principalis): Hope, and the interfaces of science, conservation, and politics. Auk 123, 1-15 (2006).
- M. Loreau et al., Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294, 804-808 (2001).
- S. Naeem, J. E. Duffy, E. S. Zavaleta, The functions of biological diversity in an age of extinction. Science 336, 1401-1406 (2012).
- B. Collen et al., Monitoring change in vertebrate abundance: The Living Planet Index. Conserv. Biol. 23, 317–327 (2009).
- W. Jetz et al., Essential biodiversity variables for mapping and monitoring species populations. Nat. Ecol. Evol. 3, 539-551 (2019)
- H. R. Akçakaya et al., Quantifying species recovery and conservation success to develop an IUCN Green List of species. Conserv. Biol. 32, 1128–1138 (2018).
- A. Toszogyova, J. Smyčka, D. Storch, Mathematical biases in the calculation of the Living Planat Index lead to overestimation of vertebrate population decline. *Nat. Commun.* **15**, 5295 (2024). S. Díaz *et al.*, Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol. Evol.* **3**, 2958–2975 (2013). D. P. Faith, Edge of existence and phylogenetic diversity. *Anim. Conserv.* **22**, 537–538 (2019). D. E. Schindler, J. B. Armstrong, T. E. Reed, The portfolio concept in ecology and evolution. *Front. Ecol. Environ.* **13**, 257–263 (2015).

- J. M. Bullock et al., Future restoration should enhance ecological complexity and emergent properties at multiple scales. Ecography 2022, e05780 (2022).
- M. W. Cadotte, K. Carscadden, N. Mirotchnick, Beyond species: Functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48, 1079-1087 (2011).
- 43. M. Cardillo, Phylogenetic diversity in conservation: A brief history, critical overview, and challenges to progress. Camb. Prisms: Extinct. 1, e11 (2023).
- A. S. L. Rodrigues, Accounting for functionality in the identification of global conservation priorities: Promises and pitfalls. Philos. Trans. R. Soc. Lond. B Biol. Sci. 380, 20230209 (2025).
- J. R. Karr, E. R. Larson, E. W. Chu, Ecological integrity is both real and valuable. Conserv. Sci. Pract. 4, e583 (2022).
- A. J. Hansen et al., Toward monitoring forest ecosystem integrity within the post-2020 Global Biodiversity Framework. Conserv. Lett. 14, e12822 (2021).
- Y. Rohwer, E. Marris, Ecosystem integrity is neither real nor valuable. Conserv. Sci. Pract. 3, e411 (2021).
- A. P. Durán et al., A practical approach to measuring the biodiversity impacts of land conversion. Methods Ecol. Evol. 11, 910–921 (2020).
- R. Lande, Genetics and demography in biological conservation. Science 241, 1455–1460 (1988).
- J. A. DeWoody, A. M. Harder, S. Mathur, J. R. Willoughby, The long-standing significance of genetic diversity in conservation. *Mol. Ecol.* **30**, 4147–4154 (2021). M. Kardos *et al.*, The crucial role of genome-wide genetic variation in conservation. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2104642118 (2021).

- C. M. McLaughlin, C. Hinshaw, S. Sandoval-Arango, M. Zavala-Paez, J. A. Hamilton, Redlisting genetics: Towards inclusion of genetic data in IUCN Red List assessments. Conserv. Genet. 26, 213–223 (2025). B. Forester, T. Lama, "The role of genomics in the future of Endangered Species Act decision-making" in The Codex of the Endangered Species Act: The Next Fifty Years, L. E. Baier, J. F. Organ, C. E. Segal, Eds. (Rowman & Littlefield, 2023).
- A. Mastretta-Yanes et al., Multinational evaluation of genetic diversity indicators for the Kunming-Montreal Global Biodiversity Framework. Ecol. Lett. 27, e14461 (2024)
- C. Moritz, Defining 'evolutionary significant units' for conservation. *Trends Ecol. Evol.* **9**, 373–375 (1994).

 A. C. Kitchener, M. A. Beaumont, D. Richardson, Geographical variation in the clouded leopard, Neofelis nebulosa, reveals two species. *Curr. Biol.* **16**, 2377–2383 (2006).
- N. J. B. Isaac, J. Mallet, G. M. Mace, Taxonomic inflation: Its influence on macroecology and conservation. Trends Ecol. Evol. 19, 464-469 (2004).
- S. Meiri, G. M. Mace, New taxonomy and the origin of species. PLoS Biol. 5, 194 (2007).
- K. A. Crandall, O. R. P. Bininda-Emonds, G. M. Mace, R. K. Wayne, Considering evolutionary processes in conservation biology. Trends Ecol. Evol. 15, 290-295 (2000)
- W. C. Funk, J. K. McKay, P. A. Hohenlohe, F. W. Allendorf, Harnessing genomics for delineating conservation units. Trends Ecol. Evol. 27, 489-496 (2012).
- D. J. Coates, M. Byrne, C. Moritz, Genetic diversity and conservation units: Dealing with the species-population continuum in the age of genomics. Front. Ecol. Evol. 6, 165 (2018).
- B. H. Daru et al., Spatial overlaps between the global protected areas network and terrestrial hotspots of evolutionary diversity. Glob. Ecol. Biogeogr. 28, 757–766 (2019).
- M. H. Meek *et al.*, Understanding local adaptation to prepare populations for climate change. *Bioscience* **73**, 36–47 (2023). Y. Kisel, T. G. Barraclough, Speciation has a spatial scale that depends on levels of gene flow. *Am. Nat.* **175**, 316–334 (2010).
- Ç. H. Şekercioğlu, Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464-471 (2006).
- S. H. Spektrolgy, intelesting awareness or avail actionized intention. *Intelligence Science* 31, 1765 (2006).

 J. Terborgh *et al.*, Tree recruitment in an empty forest. *Ecology* 89, 1757–1768 (2008).

 S. H. Anderson, D. Kelly, J. J. Ladley, S. Molloy, J. Terry, Cascading effects of bird functional extinction reduce pollination and plant density. *Science* 331, 1068–1071 (2011).

 B. H. McRae, B. G. Dickson, T. H. Keitt, V. B. Shah, Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89, 2712–2724 (2008).

 E. C. Fricke, A. Ordonez, H. S. Rogers, J.-C. Svenning, The effects of defaunation on plants' capacity to track climate change. *Science* 375, 210–214 (2022).

 J. Wooks et al. Climate design visities in dispraced politic proposes; to forest to propose the first form of the proposes.

- T. L. Weeks et al., Climate-driven variation in dispersal ability predicts responses to forest fragmentation in birds. *Nat. Ecol. Evol.* 7, 1079–1091 (2023). J. M. J. Travis et al., Dispersal and species' responses to climate change. *Oikos* 122, 1532–1540 (2013).
- J. M. Bullock et al., Human-mediated dispersal and the rewiring of spatial networks. Trends Ecol. Evol. 33, 958-970 (2018). 72.
- R. J. Fletcher et al., The prominent role of the matrix in ecology, evolution, and conservation. Ann. Rev. Ecol. Evol. Syst. 55, 423-447 (2024).
- M. C. Urban, L. De Meester, M. Vellend, R. Stoks, J. Vanoverbeke, A crucial step toward realism: Responses to climate change from an evolving metacommunity perspective. Evol. Appl. 5, 154-167 (2012).
- D. G. Hole et al., Projected impacts of climate change on a continent-wide protected area network. Ecol. Lett. 12, 420-431 (2009).
- M. C. Urban et al., Improving the forecast for biodiversity under climate change. Science 353, aad8466 (2016).
- C. Román-Palacios, J. J. Wiens, Recent responses to climate change reveal the drivers of species extinction and survival. Proc. Natl. Acad. Sci. U.S.A. 117, 4211-4217 (2020).
- J. M. Chase, A. Jeliazkov, E. Ladouceur, D. S. Viana, Biodiversity conservation through the lens of metacommunity ecology. Ann. N. Y. Acad. Sci. 1469, 86-104 (2020).
- J. Hilty et al., Guidelines for Conserving Connectivity through Ecological Networks and Corridors (IUCN, 2020).
- M. G. Betts et al., Extinction filters mediate the global effects of habitat fragmentation on animals. Science 366, 1236-1239 (2019).
- J. A. Tobias, Ç. H. Şekercioğlu, F. H. Vargas, "Bird conservation in tropical ecosystems: Challenges and opportunities" in Key Topics in Conservation Biology, D. MacDonald, K. Willis, Eds. (John Wiley & Sons, 2013), pp. 258-276.
- pp. 256–276.

 P. R. Elsen, W. B. Monahan, A. M. Merenlender, Global patterns of protection of elevational gradients in mountain ranges. Proc. Natl. Acad. Sci. U.S.A. 115, 6004–6009 (2018).

 B. M. Winger, G. G. Auteri, T. M. Pegan, B. C. Weeks, A long winter for the Red Queen: Rethinking the evolution of seasonal migration. Biol. Rev. Camb. Philos. Soc. 94, 737–752 (2019).

 C. Howard et al., Flight range, fuel load and the impact of climate change on the journeys of migrant birds. Proc. R. Soc. B 285, 20172329 (2018).

 J. P. González-Varo et al., Limited potential for bird migration to disperse plants to cooler laititudes. Nature 595, 75–79 (2021). 83.
- 85
- S. Bauer, B. J. Hoye, Migratory animals couple biodiversity and ecosystem functioning worldwide. Science 344, 1242552 (2014)
- K. R. Wotton et al., Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services. Curr. Biol. 29, 2167–2173.e5 (2019). J. A. Vickery et al., The conservation of Afro-Palaearctic migrants: What we are learning and what we need to know? Ibis 165, 717-738 (2023).
- M. D. Reynolds et al., Dynamic conservation for migratory species. Sci. Adv. 3, e1700707 (2017).
- A. Stanworth, K.-H. Peh, R. J. Morris, Linking network ecology and ecosystem services to benefit people. People Nat. 6, 1048-1059 (2024).
- J. Ollerton, R. Winfree, S. Tarrant, How many flowering plants are pollinated by animals? Oikos 120, 321-326 (2011).
- H. F. Howe, J. Smallwood, Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13, 201-228 (1982).
- P. Sethi, H. F. Howe, Recruitment of hornbill-dispersed trees in hunted and logged forests of the Indian Eastern Himalaya. Conserv. Biol. 23, 710-718 (2009).
- T.T. Caughlin et al., Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. Proc. R. Soc. B 282, 20142095 (2015).
- J. G. Rodger et al., Widespread vulnerability of flowering plant seed production to pollinator declines. Sci. Adv. 7, eabd3524 (2021).

 J. Millard et al., Key tropical crops at risk from pollinator loss due to climate change and land use. Sci. Adv. 9, eadh0756 (2023).
- J. A. Estes et al., Trophic downgrading of planet Earth. Science 333, 301-306 (2011).

- J. Ollerton, Pollinator diversity: Distribution, ecological function, and conservation. Ann. Rev. Ecol. Evol. Syst. 48, 353-376 (2017).
- T. P. Bregman et al., Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. Proc. R. Soc. B 283, 20161289 (2016).
- 100. J. H. Hatfield, C. Banks-Leite, J. Barlow, A. C. Lees, J. A. Tobias, Constraints on avian seed dispersal reduce potential for resilience in degraded tropical forests. Funct. Ecol. 38, 315-326 (2024).
- 101. M. B. Araújo, M. Luoto, The importance of biotic interactions for modelling species distributions under climate change. Glob. Ecol. Biogeogr. 16, 743-753 (2007).
- 102. A. L. Pigot, J. A. Tobias, Species interactions constrain geographic range expansion over evolutionary time. Ecol. Lett. 16, 330-338 (2013).
- 103. L. S. Comita, S. M. Stump, Natural natural enemies and the maintenance of tropical tree diversity: Recent insights and implications for the future of biodiversity in a changing world. Ann. Missouri Bot. Gard. 105,
- 104. J. Gröning, A. Hochkirch, Reproductive interference between animal species. Q. Rev. Biol. 83, 257-282 (2008).

- J. Gröning, A. Hochkirch, Reproductive interference between animal species. *Q. Rev. Biol.* 83, 257–282 (2008).
 D. Lawrence *et al.*, Species interactions alter evolutionary responses to a novel environment. *J. G. Biol.* 10, e1001330 (2012).
 A. Balmford *et al.*, Economic reasons for conserving wild nature. *Science* 297, 950–953 (2002).
 P. McCarthy *et al.*, Financial costs of meeting global biodiversity conservation targets: Current spending and unmet needs. *Science* 338, 946–949 (2012).
 C. J. Brauer *et al.*, Natural hybridization reduces vulnerability to climate change. *Nat. Clim. Chang.* 13, 282–289 (2023).
 B. C. Weeks, S. Naeem, J. R. Lasky, J. A. Tobias, Diversity and extinction risk are inversely related at a global scale. *Ecol. Lett.* 25, 697–707 (2022).
 G. W. Schuurman *et al.*, Navigating ecological transformation: Resist, accept, direct as a path to a new resource management paradigm. *Bioscience* 72, 16–29 (2022).
- 111. D. M. Leigh, A. P. Hendry, E. Vázquez-Domínguez, V. L. Friesen, Estimated six percent loss of genetic variation in wild populations since the industrial revolution. Evol. Appl. 12, 1505–1512 (2019).
- 112. M. L. Pinsky, S. R. Palumbi, Meta-analysis reveals lower genetic diversity in overfished populations. *Mol. Ecol.* 23, 29–39 (2014).
- 113. H. De Kort et al., Life history, climate and biogeography interactively affect worldwide genetic diversity of plant and animal populations. Nat. Commun. 12, 516 (2021).
- 114. M. C. Fitzpatrick, S. R. Keller, Ecological genomics meets community-level modelling of biodiversity: Mapping the genomic landscape of current and future environmental adaptation. Ecol. Lett. 18, 1–16 (2015).
- 115. O. Razgour et al., An integrated framework to identify wildlife populations under threat from climate change. Mol. Ecol. Res. 18, 18-31 (2018).
- 116. O. Razgour et al., Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. Proc. Natl. Acad. Sci. U.S.A. 116, 10418-10423 (2019).
- 117. R. A. Bay, N. H. Rose, C. A. Logan, S. R. Palumbi, Genomic models predict successful coral adaptation if future ocean warming rates are reduced. Sci. Adv. 3, e1701413 (2017).
- 118. B. R. Forester, C. C. Day, K. Ruegg, E. L. Landguth, Evolutionary potential mitigates extinction risk under climate change in the endangered southwestern willow flycatcher. *J. Hered.* **114**, 341–353 (2023). 119. D. M. Leigh *et al.*, Opportunities and challenges of macrogenetic studies. *Nat. Rev. Genet.* **22**, 791–807 (2021).

- D. O'Brien et al., Bringing together approaches to reporting on within-species genetic diversity. J. Appl. Ecol. 59, 2227–2233 (2022).
 C. Schmidt, S. Hoban, W. Jetz, Conservation macrogenetics: Harnessing genetic data to meet conservation commitments. Trends Genet. 39, 816–829 (2023).
 H. B. Shaffer et al., Landscape genomics to enable conservation actions: The California Conservation Genomics Project. J. Hered. 113, 577–588 (2022).

- 123. P. B. Pearman *et al.*, Monitoring of species' genetic diversity in Europe varies greatly and overlooks potential climate change impacts. *Nat. Ecol. Evol.* **8**, 267–281 (2024). 124. J. P. Torres-Florez *et al.*, The coming of age of conservation genetics in Latin America: What has been achieved and what needs to be done. *Conserv. Genet.* **19**, 1–15 (2018). 125. E. Gardner, Field boundary features can stabilize bee populations and the pollination of mass-flowering crops in rotational systems. *J. Appl. Ecol.* **58**, 2287–2304 (2021).
- 126. K. D. Holl et al., Applied nucleation facilitates tropical forest recovery: Lessons learned from a 15-year study. J. Appl. Ecol. 57, 2316-2328 (2020).
- 127. I. Hanski, O. Ovaskainen, The metapopulation capacity of a fragmented landscape. Nature 404, 755-758 (2000).
- 128. S. Saura, L. Pascual-Hortal, A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. Landsc. Urban Plan. 83, 91-103 (2007).
- 129. M. J. Drielsma, J. Love, S. Taylor, R. Thapa, K. J. Williams, General landscape connectivity model (GLCM): A new way to map whole-of-landscape biodiversity functional connectivity for operational planning and reporting. Ecol. Modell. 465, 109858 (2022).
- 130. R. Oyanedel, A. Hinsley, B. T. M. Dentinger, E. J. Milner-Gulland, G. Furci, A way forward for wild fungi in international sustainability policy. Conserv. Lett. 15, e12882 (2022).
- 131. A. Markandya *et al.*, Counting the cost of vulture decline—An appraisal of the human health and other benefits of vultures in India. *Ecol. Econ.* **67**, 194–204 (2008). 132. S. Soliveres *et al.*, Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* **536**, 456–459 (2016).

- S. Soliveres et al., Biodiversity at multiple tropinic levels is needed for ecosystem multifunctionality, Nature 336, 450-439 (2016).
 J. R. Patterson, T. L. DeVeault, J. C. Beasley, Integrating terrestrial scavenging ecology into contemporary wildlife conservation and management. Ecol. Evol. 12, e9122 (2022).
 S. Torabian, A. J. Leffler, L. Perkins, Importance of restoration of dung beetles in the maintenance of ecosystem services. Ecol. Solut. Evid. 5, e12297 (2024).
 R. Spake et al., An analytical framework for spatially targeted management of natural capital. Nat. Sustain. 2, 90-97 (2019).
 A. Perino et al., Rewilding complex ecosystems. Science 364, eaav5570 (2019).

- 137. J.-C. Svenning, Rewilding should be central to global restoration efforts. *One Earth* 3, 657-660 (2020).
 138. J.-C. Svenning, R. Buitenwerf, E. Le Roux, Trophic rewilding as a restoration approach under emerging novel biosphere conditions. *Curr. Biol.* 34, R435-R451 (2024).
 139. E. J. Lundgren *et al.*, Functional traits—not nativeness—shape the effects of large mammalian herbivores on plant communities. *Science* 383, 531–537 (2024).
- 140. C. Nores et al., Rewilding through inappropriate species introduction: The case of European bison in Spain. Conserv. Sci. Pract. 6, e13221 (2024).
- 141. N. Pettorelli, J. M. Bullock, Restore or rewild? Implementing complementary approaches to bend the curve on biodiversity loss. Ecol. Solut. Evid. 4, e12244 (2023)
- 142. D. S. Srivastava, M. W. Cadotte, A. A. M. MacDonald, R. G. Marushia, N. Mirotchnick, Phylogenetic diversity and the functioning of ecosystems. Ecol. Lett. 15, 637-648 (2012).
- 143. J. A. Tobias, A bird in the hand: Global-scale morphological trait datasets open new frontiers of ecology, evolution and ecosystem science. Ecol. Lett. 25, 573-580 (2022).
- 144. M. Schleuning, D. García, J. A. Tobias, Animal functional traits: Towards a trait-based ecology for whole ecosystems. Funct. Ecol. 37, 4-12 (2023).
- 145. A. L. Pigot et al., Macroevolutionary convergence connects morphological form to ecological function in birds. Nat. Ecol. Evol. 4, 230-239 (2020).
- 146. V. Gagic et al., Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proc. R. Soc. B: Biol. Sci. 282, 20142620 (2015).
- 147. J. R. Ali, B. W. Blonder, A. L. Pigot, J. A. Tobias, Bird extinctions threaten to cause disproportionate reductions of functional diversity and uniqueness. Funct. Ecol. 37, 162–175 (2023).
- 148. M. Pacifici et al., Species' traits influenced their response to recent climate change. Nat. Clim. Change 7, 205-208 (2017).
- 149. R. R. Germain et al., Species-specific traits mediate avian demographic responses under past climate change. Nat. Ecol. Evol. 7, 862-872 (2023).
 150. N. Pettorelli et al., Satellite remote sensing of ecosystem functions: Opportunities, challenges and way forward. Remote Sens. Ecol. Con. 4, 71-93 (2018).
- 151. J. Cavender-Bares et al., Integrating remote sensing with ecology and evolution to advance biodiversity conservation. Nat. Ecol. Evol. **6**, 506–519 (2022).