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How biodiversity conservation adapts to climate change: from a cross-spatial scale framework

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Climate change has emerged as one of the most significant threats to global biodiversity, and climate adaptation has become a critical component of biodiversity conservation. This paper reviews adaptive management strategies for enhancing biodiversity resilience under climate change, based on a cross-scale framework. The findings reveal that: (1) Biodiversity conservation adaptation to climate change requires a cross-spatial scale framework, which highlights the vertical interaction and interdependencies between regional, landscape, and site-level strategies. (2) Adaptive management strategies vary across spatial scales. At the regional scale, dynamic planning based on assessment and monitoring is prioritized. Landscape-scale initiatives emphasize protected areas as the core, expanding their scope while restructuring networks through corridors, stepping stone, habitat matrix permeability, and climate refugia. At the site scale, efforts focus on *in situ* and *ex situ* conservation of keystone species, along with real-time monitoring of invasive species. (3) Future challenges in biodiversity conservation under climate change may include social inequity in adaptation efforts, delayed responses in dynamic landscape conservation planning, disruptions to species's ecological networks, barriers to interdisciplinary collaboration, and insufficient attention to human-climate interactions. By highlighting the differential application of adaptation strategies across spatial scales and underscoring the critical importance of cross-scale collaboration, our findings provide important insights for advancing research and practice in biodiversity adaptation to climate change, offering a theoretical foundation and practical guidance for developing multi-level, operable climate-adaptive conservation policies.

KEYWORDS

climate change, biodiversity, adaptation, region-landscape-site scale, cross-spatial scale

1 Introduction

Global climate has changed more rapidly since 1950 than in any comparable period during the preceding million years (Stocker et al., 2013). Anthropogenic climate change now represents the most significant threat to biodiversity, significantly impacting species' phenology, distribution and abundance, and further affecting ecosystem structure, function, stability and their feedback regulation to climate change (Urban, 2015). Climate change exerts profound and multidimensional pressures on biodiversity through interconnected pathways. Rising temperatures are triggering large-scale species redistribution, with many organisms shifting poleward and upward in elevation to track suitable climates (Pecl et al., 2017). Alarming, current extinction rates now exceed background rates by 100–1,000 times, with

projected species losses of 5% at 2 °C warming and 16% at 4.3 °C (Bongaarts, 2019). Concurrently, climate-driven ecosystem degradation manifests through cascading effects: at 1 °C warming, mass coral bleaching becomes widespread (IPCC, 2002); a 2 °C increase severely disrupts most European ecosystems, drastically reducing Mediterranean plant diversity (Bakkenes et al., 2006); and beyond 3 °C, extensive forest loss is expected across Eurasia, eastern China, Canada, and the central U.S. (Scholze et al., 2006). The cumulative impacts are compounded by extreme events, as exemplified by Cyclone Idai, which reduced small herbivore populations in Mozambique by 28% within 20 months (Walker et al., 2023). Amid escalating extinction risks and ecosystem destabilization (Field et al., 2014), climate-resilient biodiversity conservation has become a global priority. The 2024 Convention on Biological Diversity (COP16) highlighted “climate change” and “biodiversity governance” as key agenda items (Climate-Diplomacy, 2024). Given that climate change exacerbates risks to both natural and human systems, advancing scientific understanding of its impacts on biodiversity and developing adaptive conservation strategies hold critical theoretical and practical significance for global biodiversity protection and international policy implementation.

Keeping track of research and practice on biodiversity adaptation to climate change will help us identify effective strategies. Over the past two decades, scientists have conducted a systematic reviewing of adaptation strategies proposed in existing research. Since Heller and Zavaleta (2009) comprehensively reviewed relevant research from 1975 to 2007 and categorized adaptation strategies (Heller and Zavaleta, 2009), McLaughlin et al. (2022) further traced research from 2007 to 2017 and found that, in comparison, climate change refugia, climate-adaptive assisted migration, and climate-adaptive genetics are three of the most latest and robust strategies for coping with climate change (McLaughlin et al., 2022). (iii) There are also reviews for a particular adaptation strategy, such as climate change adaptation planning for biodiversity conservation (Watson et al., 2012), land-use planning-based climate change adaptation (Schmitz et al., 2015), spatial planning for climate change adaptation (Reside et al., 2018), and habitat connectivity (Keeley et al., 2018). Nevertheless, biodiversity adaptation to climate change is a systematic process, reviewing existing research and practice based on an integrated framework is necessary. For example, Mawdsley et al. (2009) constructed an integrated framework for a taxonomy of natural resource management actions, and applied it to review existing research on biodiversity adaptation to climate change (Mawdsley et al., 2009).

The existing reviews have provided important inspiration for this paper, but it must also be realized that merely reviewing biodiversity adaptation strategies is not enough. An adaptation strategy may be applicable at the national or local government levels, but is too broad for protected areas (PAs), parks, watersheds, etc. In comparison, adaptation strategies that work for one particular species may be too granular for the landscape scale. Based on the above, current reviews of climate adaptation strategies remain overly generalized, and that it is essential to review and assess existing research and practice at different spatial scales. How can adaptive management strategies across multiple spatial scales effectively enhance the adaptive capacity of biodiversity to climate change? In contrast to approaches that classify conservation actions either by type (e.g., legal policies or direct species management) (Mawdsley et al., 2009) or by the nature of the

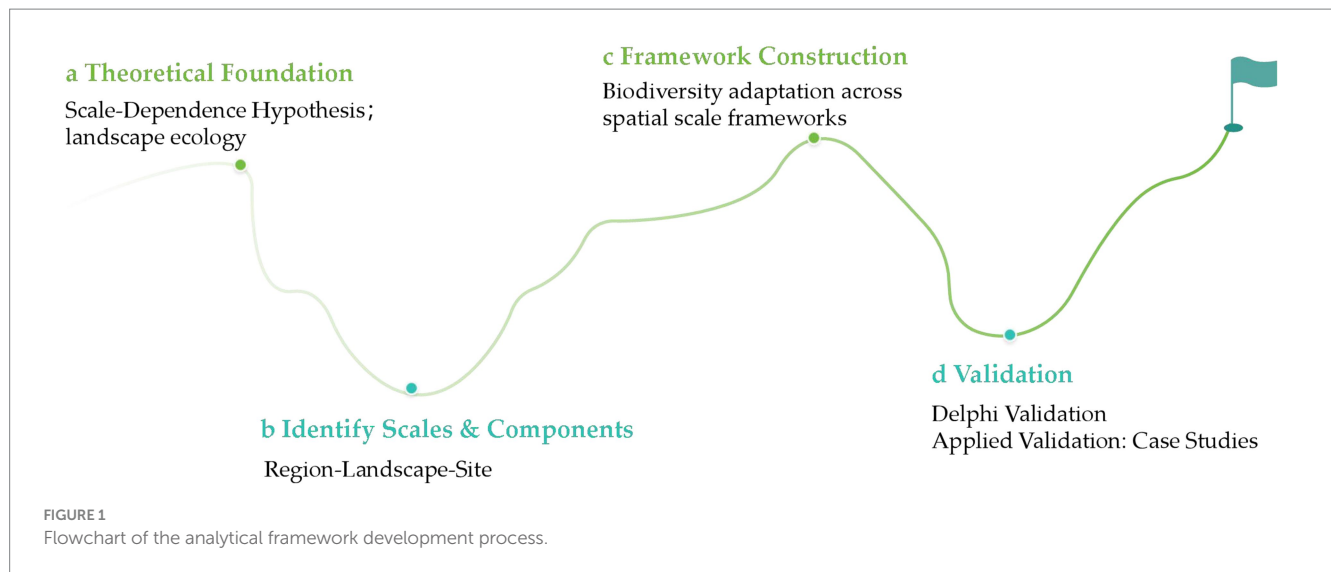
strategy itself (e.g., modifying conservation plans) (Heller and Zavaleta, 2009), this paper establishes a multi-scale analytical framework for biodiversity adaptation to climate change based on landscape ecology, systematically reviewed the adaptive management strategies of biodiversity at different spatial scales of region-landscape-site, with a specific focus on synergistic interactions among three critical scales (regional, landscape, and site) to enhance ecological resilience. Furthermore, we systematically synthesize existing research and practical interventions in climate-adaptive biodiversity conservation across these scales, while identifying key challenges for future research.

2 Adaptation of biodiversity to climate change cross spatial scales

Based on the scale-dependence hypothesis (Chase et al., 2018), this study systematically identifies core adaptive management components across regional, landscape, and site scales under the guidance of landscape ecology and existing theoretical research. On this basis, a cross-scale biodiversity adaptation framework was constructed. The framework was preliminarily validated using the Delphi method and further applied in typical practical cases to examine its explanatory power and applicability (Figure 1).

2.1 Adaptation as a continuum of resistance, resilience and transformation

The systematic conceptualization of biological adaptation originates in Darwin's theory of natural selection (1859), which emphasized organisms' development of adaptive traits through genetic variation and environmental selection pressures (Darwin, 1859). Autonomous adaptation initially manifested through evolutionary responses to natural selection, exemplified by beak morphology changes in Galápagos finches (Grant and Grant, 2002). In the early 20th century, adaptation theory expanded to include niche differentiation and coevolution, such as the Red Queen hypothesis (Valen, 1973), though remaining confined to natural ecological processes. MacArthur and Wilson's (1967) theory of island biogeography significantly advanced understanding of species adaptation mechanisms (MacArthur and Wilson, 1967), laying foundations for conservation biology. The 1990s marked a pivotal transition period in which adaptation evolved into a cross-disciplinary policy instrument through the First Assessment Report by the Intergovernmental Panel on Climate Change (IPCC) and the United Nations Framework Convention on Climate Change (UNFCCC) (IPCC, 1990; UN, 1992), extending its application to disaster management, political ecology, rights protection, and food security (Smit and Wandel, 2006). While long considered as a component of ecological resilience, adaptation's formal integration into mainstream biodiversity conservation frameworks occurred in the early 21st century. A critical turning point emerged with the 2010 Strategic Plan for Biodiversity (CBD, 2010), which for the first time explicitly incorporated adaptation into biodiversity conservation policies. Building upon this foundation, the IPCC Sixth Assessment Report (AR6, 2022) advanced the conceptual framework by proposing a “resistance-recovery-transformation” adaptation continuum (IPCC,



2022), systematically emphasizing the critical role of proactive human intervention in biodiversity conservation.

In contemporary conservation biology, the adaptation concept has evolved from its initial focus on innate species adaptability (MacArthur and Wilson, 1967) to policy-driven proactive strategies (CBD, 2010; IPCC, 2022) addressing anthropogenic climate impacts on biodiversity. This evolution marks a paradigm shift from studying natural ecological process to governing socio-ecological system (Sgrò et al., 2011). As biodiversity adapts to climate change, adaptation can be viewed as a continuum of resistance, recovery, and transformation, where resistance refers to the maintenance of the existing state from climate disturbances, while recovery is the process of returning to a state that was previously maintained after disturbance (Hodgson et al., 2015), and transformation means enabling or facilitating the transition to new conditions (Peterson St-Laurent et al., 2021). Policy interventions should account for ecosystem characteristics to enhance biodiversity's capacity to recover from rapid climate change while maintaining ecological functions.

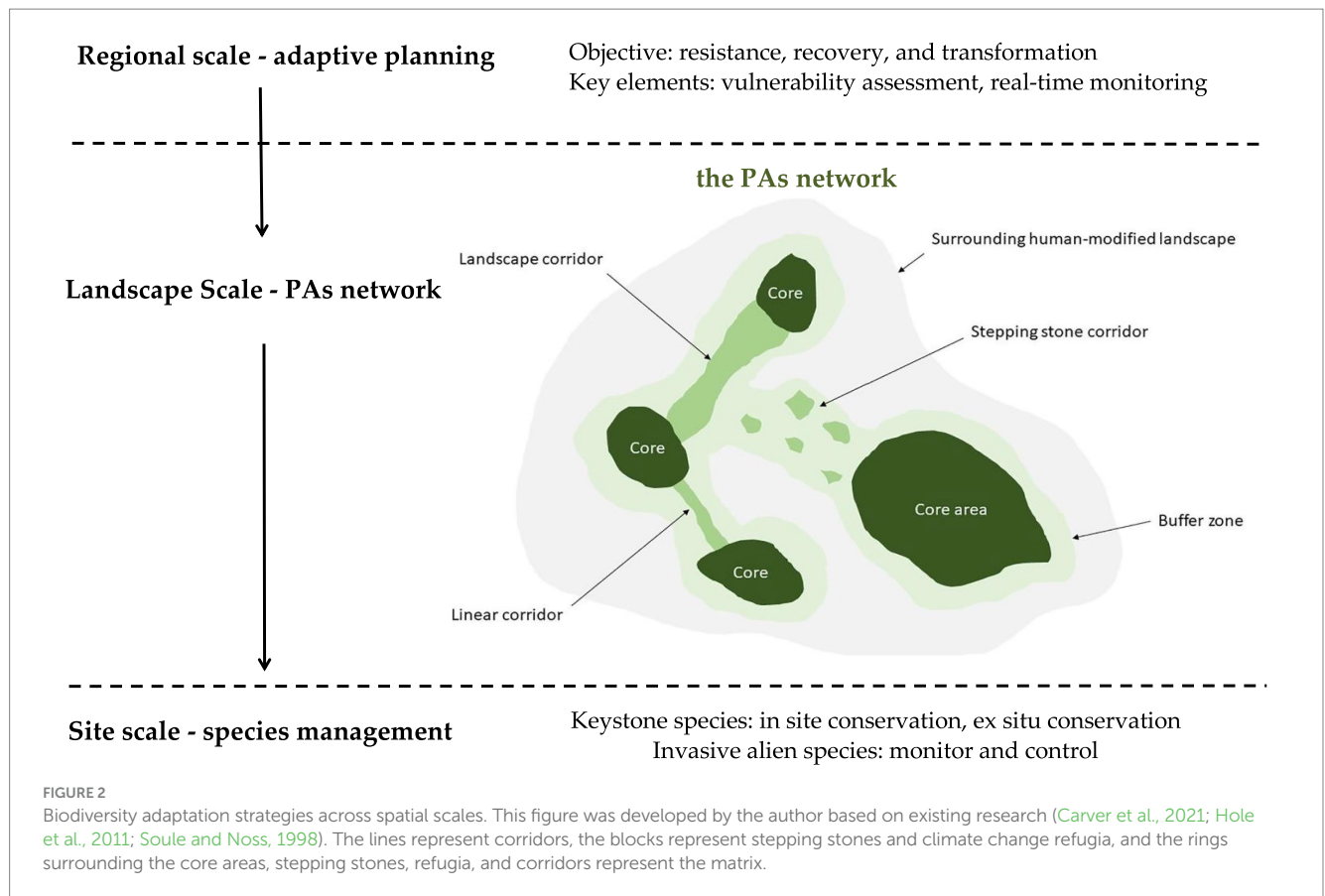
2.2 Biodiversity adaptation across spatial scale frameworks

Climate change impacts on biodiversity manifest through distinct scale-dependent processes (Ackerly et al., 2010). These impacts are simultaneously determined by macro-scale climate change patterns and mediated through species-ecosystem interactions (Wu and Li, 2006), necessitating an integrated cross-scale approach to biodiversity adaptation strategies (Phillips et al., 2025; Willis and Bhagwat, 2009). Cross-scale biodiversity adaptation refers to the multi-tiered conservation responses across spatial scales (regional, landscape, and site levels) in the context of climate change (Poiani et al., 2000), designed to address climate impacts operating at multiple scales. Landscape ecology offers the foundational theoretical framework for understanding these cross-scale interactions: (i) The spatial heterogeneity and diversity theory emphasizes the non-uniform distribution of landscape elements and their influence on ecological processes. Under climate change, biodiversity conservation targets similarly demonstrate marked spatial heterogeneity. (ii) The

hierarchical patch dynamics paradigm conceptualizes ecosystems as dynamic mosaics of multi-level patches interconnected through ecological processes (Zhang et al., 2013). This hierarchical structure necessitates conservation strategies that establish cross-scale feedback mechanisms, where regional climate patterns influence landscape-scale habitat distribution, while site-specific microhabitat conditions reciprocally modulate local climatic features.

Figure 2 illustrates an operational (though imperfect) framework illustrating biodiversity adaptation across three spatial scales. Specifically: (i) The regional scale encompasses broader geographical areas containing multiple landscape types (Ekroos et al., 2016). (ii) The landscape represents habitat complexes with environmental gradients supporting multiple populations (Poiani et al., 2000). (iii) The site scale refers to homogeneous habitat patches supporting specific populations (Norris et al., 2020). In practice, regional biodiversity conservation planning needs to respond to global climate change and implement vulnerability assessments, conservation target setting, spatial project planning, and monitoring throughout implementation based on local resources and institutional capacity. The landscape scale emphasizes maximizing species and ecosystem diversity to enhance resilience. Specifically, this involves connecting PAs through corridors, stepping stones, and landscape matrix, supplemented by climate change refugia to aid species persistence and recovery, thereby enhancing the protected area network connectivity and improving landscape resilience. The site scale focuses on keystone species and invasive species, with conservation efforts prioritizing in-situ conservation while incorporating ex-situ measures; invasive species monitoring requires continuous assessment of their impacts on genetic diversity and ecosystem integrity.

The conservation initiative in Yampa River Basin in Colorado, USA, exemplifies the application of this framework (Poiani et al., 2000). Initially, conservation efforts focused on protecting rare species. Since 1986, The Nature Conservancy (TNC) has implemented measures such as riparian land acquisition and vegetation restoration, primarily to protect the globally rare *Acer negundo*–*Populus angustifolia*/Cornus sericea riparian forest. In the late 1990s, with improved understanding of riparian ecosystem dynamics, TNC's conservation focus shifted from a single forest type to conserving the entire riparian mosaic ecosystem, expanding conservation strategies



from the site to the landscape level. After 2010, the Yampa River Basin was incorporated into the Upper Colorado River basin-wide conservation network, realizing the “Networks of Reserves” concept.

2.3 Cross-scale synergy in biodiversity adaptation

2.3.1 How to achieve synergy?

The core of the “regional-landscape-site” cross-scale framework lies in its multi-scale systemic integration, overcoming the limitations of traditional single-scale conservation approaches to develop comprehensive solutions for climate change complexities (Figure 3). This framework emphasizes vertical interactions and interdependencies, responding to climate change uncertainties through both spatial cascades and policy implementation.

- (a) In terms of spatial scales, vertical integration manifests through a species-landscape-region planning hierarchy. While site-scale species protection yields local benefits, it faces challenges in achieving broader ecosystem functional adaptation goals. Conversely, landscape-scale approaches achieve functional integration through ecological networks (corridors/refugia), yet face land-use conflicts (Mendonça et al., 2021), governance fragmentation (Dorst et al., 2022), and multi-stakeholder coordination challenges (Kauark-Fontes et al., 2023). Large-scale interventions require coordination at a broader regional scale. Scientific understanding of cross-scale adaptation

challenges helps avoid maladaptive practices (Schuldt et al., 2023).

- (b) In terms of implementation, vertical interaction combines top-down resource allocation and policy dissemination with bottom-up feedback mechanisms across administrative levels (Kauark-Fontes et al., 2023; Puskás et al., 2021). The goals, geographical scope, practical measures, and implementation processes of biodiversity adaptation at the region-landscape-site scales are mutually matched (Table 1). Conceptualized as an implementation cycle, climate adaptation involves four iterative phases: planning, design, implementation, and engineering management and maintenance (Mirsafa et al., 2025). Specifically: (i) The planning stage focuses on the regional level, aiming to maintain the integrity and authenticity of the regional ecosystem. This stage involves planning across broad geographical areas spanning different landscapes, including the identification and diagnosis of macro-level issues, the setting of overall adaptive goals, and the specific layout of working units and sub-projects. (ii) The design stage focuses on the landscape level, aiming to maintain the integrity of the structure and function of ecosystems. In this stage, detailed designs of working units (e.g., protected area networks) within a complex of multiple ecosystems are required, along with the formulation of corresponding specific indicator systems and standards. (iii) The implementation stage takes place at the site level, achieving dynamic balance of the matrix ecosystem through species management. Specific project construction within species habitats requires the determination of adaptive

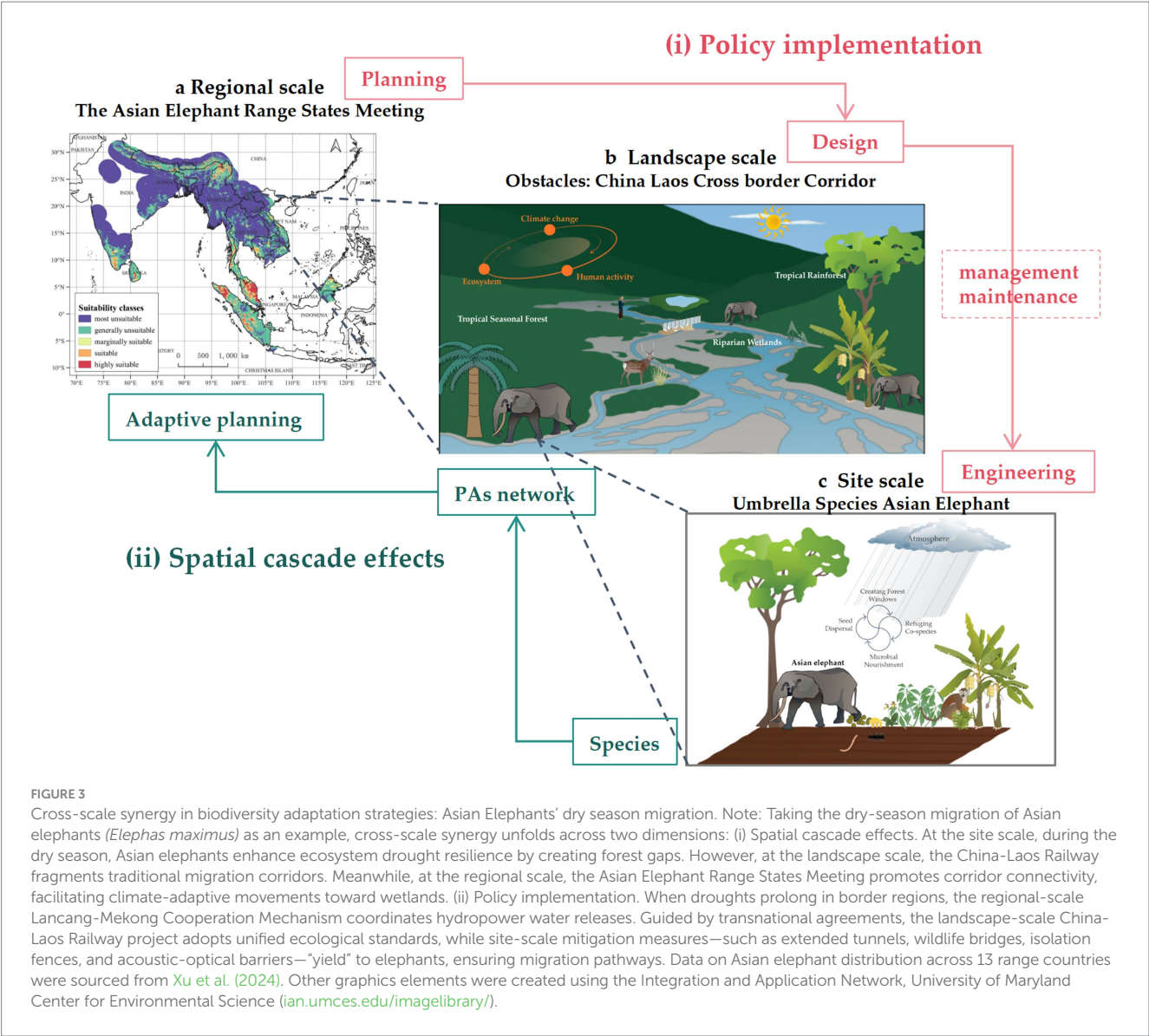


FIGURE 3 Cross-scale synergy in biodiversity adaptation strategies: Asian Elephants' dry season migration. Note: Taking the dry-season migration of Asian elephants (*Elephas maximus*) as an example, cross-scale synergy unfolds across two dimensions: (i) Spatial cascade effects. At the site scale, during the dry season, Asian elephants enhance ecosystem drought resilience by creating forest gaps. However, at the landscape scale, the China–Laos Railway fragments traditional migration corridors. Meanwhile, at the regional scale, the Asian Elephant Range States Meeting promotes corridor connectivity, facilitating climate-adaptive movements toward wetlands. (ii) Policy implementation. When droughts prolong in border regions, the regional-scale Lancang–Mekong Cooperation Mechanism coordinates hydropower water releases. Guided by transnational agreements, the landscape-scale China–Laos Railway project adopts unified ecological standards, while site-scale mitigation measures—such as extended tunnels, wildlife bridges, isolation fences, and acoustic-optical barriers—“yield” to elephants, ensuring migration pathways. Data on Asian elephant distribution across 13 range countries were sourced from Xu et al. (2024). Other graphics elements were created using the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

TABLE 1 Comparison of cross scale management strategies for biodiversity adaptation to climate change.

Scale	Objective	Geographical scope	Process	Practical measure	Examples
Region	Integrity and authenticity of the regional ecosystems	Broader geographical areas spanning different landscapes	Planning	Adaptive planning for a group of PAs network	National Biodiversity and Climate Change Action Plan 2004–2007 (Australia)
Landscape	Integrity and stability of natural ecosystems	Complex of multiple ecosystems	Design	Reconstruct PA network	the Chesapeake Bay Program; the Natura 2000 network
Site	Dynamic balance of matrix ecosystems	Habitats of homogeneous populations	Implementation	Species management	Botanical garden; Seed bank

Organized by authors.

measures based on species types and their implementation. (iv) Additionally, the management and maintenance stage covers monitoring and evaluation, adaptive management, and supervision and inspection throughout the entire process.

Biodiversity conservation across different scales works in synergy with each other and is interconnected at each level, forming a cross - scale spatial three - dimensional network to achieve collaboration.

2.3.2 Why we need synergistic integration?

The primary advantages of vertical interactions and inter-dependencies are reflected in the ecological linkages across spatial scales and the hierarchical transmission and information feedback mechanisms in implementation.

- (a) Ecological interdependencies enable cross-scale conservation coordination, forming functional ecological networks that enhance the overall efficacy of biodiversity adaptation strategies. For instance, at the regional scale, climate models can identify refugia, providing a scientific basis for the design of corridors at the landscape scale. In turn, the construction of ecological networks at the landscape scale creates migration pathways for species conservation at the site scale.
- (b) In terms of governance mechanisms, hierarchical transmission and information feedback mechanisms optimize vertical governance structures and strengthen the effectiveness of policy implementation, ensuring the scientific and operational nature of cross-scale decision-making. In horizontal cooperation, environmental departments are often the leaders in formulating national biodiversity strategy policies, while other departments (i.e., transportation, energy, waste, drainage, and water) act as supporters. Planning among departments is mostly fragmented, and policy integration always faces conflicts of interest. This leads to isolated planning and mutual buck-passing among functional departments (Kauark-Fontes et al., 2023). For example, Bicentenario Park was envisioned as a transitional space connecting the old city park and the historic center of Bogotá, Colombia. However, stakeholder coordination failures have stalled construction progress (Fixsen, 2018). Even at global scales, protracted negotiations over Convention on Biological Diversity (CBD) funding mechanisms further exemplify these governance challenges. Conversely, the Chesapeake Bay Program in the United States and the Natura 2000 network in Europe demonstrate the potential for coordinated conservation across spatial scales. The Chesapeake Bay Program guides the restoration and protection of North America's largest estuary through a regional partnership.¹ Similarly, the Natura 2000 network integrates over 27,000 PAs across member states through standardized monitoring and management frameworks.² These cases underscore that institutionalized cross-scale coordination is prerequisite for effective biodiversity governance.

2.3.3 Critical gaps in synergistic implementation

The critical gaps in biodiversity adaptation strategies across spatial scales are as follows:

- (a) Assessment of problem-governance scale alignment. Effective cross-scale management first requires a clear distinction between the spatio-temporal scale at which problems occur (problem scale) and the institutional scale at which governance is implemented (governance scale), and an assessment of the degree

of alignment between the two (Padt et al., 2014). Many countries face horizontal mismatches between internal governance scales and the scale of climate change impacts. For example, there is inconsistency between the boundaries of river basins such as the Rhine, Meuse, or Scheldt (problem scale) and the administrative boundaries of member states (governance scale) in the European Union region (Dewulf et al., 2015).

- (b) Identification of ecological cascades across spatial scales. For instance, refuge planning at the regional scale needs to be coordinated with ecological corridors at the landscape scale and habitat restoration at the site scale (Phillips et al., 2025). However, there are still deficiencies in identifying and integrating ecological cascades across spatial scales (Le Provost et al., 2023; Li et al., 2025). In geographical modeling, the nonlinear characteristics of scale transformation and cross-scale interactions pose challenges to integrating multi-level ecological effects (Peters et al., 2007). For example, simple upscaling-downscaling based on traditional hierarchical theory cannot fully explain the complex interactions between different scales (Gonzalez et al., 2020; Koo, 2009). This makes it difficult to accurately predict ecosystem behavior and dynamics in cross-scale analyses, thereby limiting the synergy between conservation measures at different scales.
- (c) Policy implementation via vertical integration. To match policy practice with the scale of biodiversity conservation goals, it is necessary to (i) coordinate and integrate across levels under the same objective, (ii) share information and resources within appropriate scopes, and (iii) to facilitate the resolution of cross-boundary issues by connecting governance systems at different scales. Current policy implementation not only lacks coordination across different levels of jurisdiction but also faces temporal scale mismatches. That is, adaptation strategies that require long-term implementation cycles face challenges due to the tendency to pursue short-term economic benefits under the fixed political turnover cycles of governments (Kettunen and Ten Brink, 2012). The difficulty in effectively coordinating governance needs at different scales during policy implementation affects the achievement of biodiversity conservation goals.
- (d) Dynamic adaptive management. Dynamically adjusting management strategies based on multi-scale ecological monitoring data is key to biodiversity conservation. For example, the Dutch "Room for the River" program dynamically adjusts the setback distance of dikes based on annual flood simulations (Zevenbergen et al., 2015). However, there are still deficiencies in dynamic adaptive management, and the linkage mechanism between long-term dynamic monitoring and strategy adjustment has not yet been established (Zarzuelo Romero et al., 2025), which limits the flexibility and effectiveness of biodiversity adaptation strategies.

3 Regional-scale adaptation planning provides top-level design

3.1 Practices of adaptive planning

Adaptive planning provides a systematic framework for biodiversity adaptation through objective-driven resource

¹ <https://www.chesapeakebay.net/>

² <http://natura2000.eea.europa.eu/>

allocation (Reside et al., 2018). Robust regional-scale adaptive planning should incorporate the following features: reversibility, preservation of future options, resistance to a variety of impacts, and permission for mid-course adjustments (Wilby and Vaughan, 2011). Effective planning must simultaneously address multiple interacting drivers of biodiversity loss, as climate change acts synergistically with habitat degradation, soil loss, nitrogen enrichment and acidification, single-focus efforts risk exacerbating the others. For example, the Kyoto Protocol addresses emission reduction plans, the Clean Development Mechanism, carbon sequestration, biodiversity conservation and human livelihoods (UNFCCC, 1997). For adaptive planning to remain flexible and robust, assessing species vulnerability and continuous real-time monitoring are key (Sutherland, 2006).

In 2002, the Strategic Plan of the CBD called for the integration of biodiversity concerns into relevant national sectoral and cross-sectoral plans, programs and policies. Developed countries and some large developing biodiversity powerhouses have placed a high priority on adaptive planning for biodiversity to climate change. Common categories of adaptive planning include the following: (i) Integrating climate adaptation into overall national development planning, which is the choice of most countries. For example, China has consistently included ecosystems as a key area of adaptation to climate change in *A Review of China's Climate Change Policies and Actions* (2022), *National Strategy for Climate Change Adaptation 2035 and National Plan for Climate Change (2014–2020)*. (ii) Embedding adaptation within existing sustainability frameworks, covering sectoral domains spanning disaster mitigation, water security, public health, environmental management, energy and national security (IPCC, 2022; UNEP, 2023). (iii) Developing dedicated adaptation plans. Australia was the first country in the world to issue a dedicated action plan for biodiversity conservation, and was the first to issue National Action Plan on Biodiversity and Climate Change, which integrated conservation and adaptation of biodiversity to climate change into key strategic planning (Booth, 2012), and developed adaptation strategy in Biodiversity and Climate Adaptation in Australia.

Globally, countries are issuing biodiversity-related national strategies or plans to respond to climate change. Developed economies concentrate planning efforts on climate change mitigation, deploying highly specified and operational initiatives, while developing countries prioritize adaptation objectives (UNEP, 2023). However, economic development priorities limit developing nations to framework-level plans that remain largely conceptual, failing to address current challenges. As the most climate-vulnerable nations, developing countries require: (i) implementation of the common but different responsibility (CBDR) principle to ensure climate justice, (ii) Global Climate Change Initiative (GCCII)-type mechanisms for equitable development (Persson et al., 2009), and (iii) institutional strengthening with adequate financing. In Australia, the Council of Ministers for Natural Resource Management leads adaptive planning, while the National Institute for Climate Change Adaptation develops policy guidance tools, and the Australian Biodiversity Fund provides financial security by establishing eco-banks that implement payments for ecosystem/environmental services (PES) (Salzman et al., 2018).

3.2 Crucial components of adaptive planning

Numerous implementation frameworks for adaptive planning have been proposed in existing research and practice: the Adaptation for Conservation Targets (ACT) (Cross et al., 2012), Climate-Smart Conservation (CSC) (Stein et al., 2014), and Portfolio Decision Analysis (PDA) (Convertino and Valverde, 2013) frameworks. However, from a process perspective, biodiversity adaptation planning generally follows a cyclical “Assess-Plan-Implement-Monitor” process (Watson et al., 2012). Specifically, during the assessment phase, risk and vulnerability analyses are conducted; the planning phase develops adaptive strategies; the implementation phase implements engineering, technological, and institutional measures; and the monitoring and adjustment phase utilizes monitoring data for subsequent dynamic optimization (Abrahms et al., 2017). To maintain flexibility and robustness in adaptive planning, various analytical frameworks and tools are employed, such as Robust Decision Making (Yousefpour and Hanewinkel, 2016), Iterative Risk Management (Döll and Romero-Lankao, 2017), and Scenario Planning (Star et al., 2016). Throughout the planning cycle, understanding and assessing species vulnerability and maintaining continuous real-time monitoring are crucial (Maris and Béchet, 2010; Sutherland, 2006). Here, monitoring serves as the linchpin connecting cyclical adaptive planning by: (i) providing baseline data for pre-implementation assessment and planning design; (ii) enabling post-implementation evaluation of management effectiveness; and (iii) informing future decision-making (Williams and Brown, 2012). The interdependent relationship between assessment and monitoring is particularly noteworthy, while assessment relies on monitoring data, monitoring ultimately serves assessment needs within this iterative framework.

3.2.1 Assessing species vulnerability

According to the IPCC (2007), the vulnerability of species to climate change encompasses three dimensions: exposure, susceptibility, and adaptive capacity (IPCC, 2007). (i) Exposure refers to the degree to which species are exposed to significant climate change, such as the proportion of species in regions experiencing rapid climate change. Generally, the faster the rate of climate change and the greater its intensity and frequency, the higher the exposure of species in that area. (ii) Susceptibility indicates the degree to which species are affected by climate hazards, determined by their intrinsic biological characteristics and emphasizing the outcomes of climate change impacts, such as species extinction or reduced abundance due to climate influences. (iii) Adaptive capacity denotes the ability of organisms to adjust to, exploit, and respond to potential damages, opportunities, or consequences (McCarthy et al., 2001). The intersection of high susceptibility, high exposure, and low adaptive capacity represents the greatest vulnerability (Hole et al., 2011).

Understanding species vulnerability under a range of potential future scenarios is important due to the uncertainty in climate change projections and in species, ecosystem and human responses. On one hand, direct threats to biodiversity from climate change may include: changes in phenology, changes in species distribution shifts, community composition alterations, ecosystem function changes and loss of living space. On the other hand, human responses to climate change also have an impact on biodiversity, mainly in the agriculture, water, health and energy sectors. For example, upslope shifts in cultivation due to climate (Warner et al., 2009). Glacial retreat due to climate change is significantly

reducing dry season flows in glacial rivers, prompting the construction of upstream reservoirs to ensure adequate flows for hydroelectric power generation and downstream agricultural needs, which may reduce the diversity and abundance of organisms along the way (Vergara et al., 2007). In addition, using biofuels as an alternative resource is seen as a way to reduce greenhouse gas emissions, while crop-based biofuel production leads to the conversion of rainforests, savannas, grasslands and other natural ecosystems to agricultural land, which generates significant carbon debt and causes widespread degradation of natural ecosystems. These indirect threats can be as serious as, or even exceed in scale and scope the direct threats, while further affecting policy feasibility (Fargione et al., 2008).

Assessing species vulnerability based on this understanding of vulnerability components is an important element of adaptation planning. For understanding and reconciling the expected interactions of the various elements, Williams et al. (2008) have integrated a working framework for species vulnerability assessments, which associates the interactions between vulnerability, exposure and adaptive capacity to guide biodiversity adaptation to climate change (Williams et al., 2008). Guided by the theoretical framework, identifying interactions between vulnerability, exposure and adaptive capacity and estimating vulnerability are the next important task (Pacifi et al., 2015). Based on the consideration of species distributional changes, population changes and extinction potential (Pacifi et al., 2015), methods for assessing species vulnerability are categorized into correlative, mechanistic, trait-based and combined approaches (Table 2).

- (a) Correlative approaches are the most widely used, mainly based on observed species distributional changes in relation to climate change to predict the possible future suitable distribution areas of species. Species distribution models (SDMs), in particular, emphasize data-driven projections of potential distributional shifts (Jakubská-Busse et al., 2024). Employing an ensemble of SDMs under the RCP8.5 scenario, Dawe and Boutin (2016) projected that the climatically suitable habitat of the white-tailed deer (*Odocoileus virginianus*) would expand northward across North America by 2050 (Dawe and Boutin, 2016). Dynamic vegetation models (DVMs) simulate climate-driven vegetation succession (Heffernan et al., 2024). Yu et al. (2014) coupled the LPJ-GUESS model with outputs from 19 GCMs under RCP8.5 and demonstrated that evergreen broad-leaved forests are projected to replace deciduous forests in eastern China by 2100 (Yu et al., 2014). Climate-trajectory models highlight species' capacity to persist and disperse by comparing future climatic analogues with current conditions. Ohlemüller et al. (2006) quantified the spatial extent of analogous and non-analogous climates across Europe to evaluate species' adaptive capacity under climate change (Ohlemüller et al., 2006). While correlative approaches efficiently predict future habitat suitability, their reliability is contingent upon robust model selection and high-resolution climatic data (Elith and Leathwick, 2009) and may overlook biotic interactions influencing adaptive capacity (Meier et al., 2011).
- (b) Mechanistic approaches focus on quantifying the probability of extinction under climate change by explicitly incorporating species-specific traits, physiological tolerances, and habitat interactions into viability assessments. Population viability analysis (PVA) exemplifies this strategy; it integrates

physiological thresholds and the stochasticity of climatic events to estimate extinction risk, with particular emphasis on endangered taxa. Using PVA, Vargas et al. (2007) demonstrated that an increase in El Niño frequency elevates the probability of population collapse for the Galápagos penguin (*Spheniscus mendiculus*) to 78% within the next 100 years (Vargas et al., 2007). Although mechanistic approaches are powerful in integrating physiological and behavioral mechanisms underlying extinction risk, they demand extensive data and remain challenging to couple with non-climatic degradation (Foden et al., 2016).

- (c) Trait-based assessment (TBA) refers to assessing the potential climate change impacts on a species by identifying the population, ecological niche and habitat characteristics of individual species through literature surveys, data compilation and expert consultation (Aguirre-Gutiérrez et al., 2025). A species is considered to have limited adaptive capacity if its habitat is within a restricted elevational range, if it has low genetic diversity or if it is dependent on only a few prey or host species. Applying this framework to the world's avifauna, Foden et al. (2013) identified alpine endemics such as the Himalayan Snowcock (*Tetraogallus himalayensis*) as highly vulnerable because of their restricted altitudinal range and weak dispersal ability (Foden et al., 2013). Although TBA translates functional attributes into quantitative vulnerability scores, the weighting of individual traits requires expert calibration to minimise subjectivity.
- (d) Combined approaches integrate correlative, mechanistic and TBA in a complementary manner to meet empirical needs. Pearson et al. (2014) coupled SDMs with PVA and demonstrated that dispersal barriers can trigger local extinctions of European amphibians even within climatically suitable habitats; such integration reduces predictive uncertainty, yet it demands extensive cross-disciplinary data support (Pearson et al., 2014).

3.2.2 Real-time monitoring throughout the process

Monitoring serves as a critical component of adaptive planning implementation, providing early warnings for emergent climate risks and establishing empirical bases for conservation effectiveness evaluation, with its outcomes requiring real-time integration into the planning revision process (Corelli et al., 2024). Specifically, monitoring objectives can be operationalized through three key dimensions: (i) Understanding how ecosystems, habitats, and species respond to climate change while identifying compounding stressors that may exacerbate these responses; (ii) Generating data for model development and validation to enhance predictive capacity for climate adaptation scenarios; (iii) Assessing the effectiveness of policy and management interventions (Bongaarts, 2019). As a representative case study, the European Biodiversity Observation Network (EU BON) project (2012–2017) established a continent-scale monitoring infrastructure through standardized permanent plots (accessible via <https://monitoring.europabon.org>), systematically recording species abundance, phenology, and microclimate data to analyze climate-land use interactions. The longitudinal datasets enabled refinement of species distribution models and evaluation of Natura 2000 PAs' capacity to accommodate climate-induced species range shifts (EU BON, 2017).

TABLE 2 Biodiversity vulnerability assessment methods.

Categories	Methods	Description	Identification	Examples
Correlative approaches	Species distribution models (SDMs)	Project future species distributions based on current distribution, abundance data and climate conditions	Sensitivity; exposure	Early and Sax (2011)
	Dynamic vegetation models (DVMs)	Process-based simulations of vegetation functional, structure and distribution under climate change	Sensitivity	Elith and Leathwick (2009)
	Climate-path models	Predict species' migration pathways by assessing populations' viability and dispersal capacity	Sensitivity.	Yu et al. (2014)
Mechanistic approaches	Population viability analysis (PVAs)	Spatially explicit modeling of population viability using species-specific demographic and environmental drivers	Sensitivity; exposure	Vargas et al. (2007)
	Ecological niche models (ENMs)	Predict extinction-risk areas based on species-habitat interactions	Sensitivity; exposure; adaptability	Morin and Thuiller (2009)
	Metapopulation models	Model distribution change for species using fragmented or patchy habitat networks	Sensitivity; exposure; adaptability	Wilson et al. (2009)
Trait-based assessment	Trait-based assessment (TBA)	Qualitative assessment of the impact of climate change on certain species	Sensitivity; exposure	Spencer et al. (2019)
Combined approaches	Assessment based on generic life history	Combine ecological niche models with demographic models	Sensitivity; exposure	Pearson et al. (2014)
	Climate Change Vulnerability Index (CCVI)	Assess regional exposure (e.g., temperature and humidity) and future changes in suitable habitat under future climate change and evaluating species vulnerability	Exposure; adaptability	Siegel et al. (2014)
	Climate Change Vulnerability Assessment (CCVA)	Evaluate extinction risk considering species' sensitivity (habitat/phenology), exposure (temperature/rainfall), and resilience (migration/ evolution)	Sensitivity; exposure; adaptability	Foden et al. (2016)
	System for Assessing Vulnerability of Species (SAVS)	Questionnaire-based assessment of climate change impacts on habitat, phenological, and interpopulation dynamics	Sensitivity; exposure	Bagne et al. (2011)

Operationalizing sustained monitoring requires the iterative execution of three core tasks: (i) Standardization of indicator systems. Standardized monitoring based on the Essential Biodiversity Variables (EBVs) enables comparable metrics across genetic, species, and ecosystem levels, facilitating cross-project data integration and trend analysis ([Geijzendorffer et al., 2016](#)). For instance, the SoilBON network employs microbial diversity and soil organic carbon EBVs to assess policy impacts on subsurface biota, with springtail (*Collembola*) abundance serving as a rapid indicator of soil quality ([Guerra et al.,](#)

[2021](#)). Likewise, the Global Coral Reef Monitoring Network adopts hard coral cover, macroalgal canopy cover, and fish diversity and abundance as three robust EBVs for reef health assessment ([Obura et al., 2019](#)). (ii) Multi-scale data integration and model validation. Species, ecosystem, climatic and remotely sensed data collected at nested scales are assimilated into analytical models to enhance the resolution of interaction effects ([Jetz et al., 2019](#)). [Rogers et al. \(2025\)](#) integrated multi-scale data via zero-inflated Bayesian regression to quantify the joint influence of climate and land use on freshwater fish

assemblages in the northeastern United States (Rogers et al., 2025). (iii) Data sharing and attribution analysis. Scientifically rigorous designs facilitate seamless data exchange, enabling the timely detection of natural trends and extreme events while disentangling causal pathways. The Colorado Parks and Wildlife agency exemplifies this approach through the Colorado Beaver Activity Mapper, which fuses: GPS-mapped beaver dam, citizen science activity reports submitted via the Engage CPW platform, and ecological process data from interagency portals to identify the drivers of beaver–human conflict dynamics (CPW, 2025; Longwell, 2025).

Moreover, the protracted nature of climate change and the persistence of statistical noise necessitate long-term monitoring programs (Leung and Gonzalez, 2024). Most environmental time series require extended periods before underlying trends or variable relationships achieve statistical significance. Many ecological responses—including species migration and community succession—as well as cyclical climatic phenomena such as the El Niño, unfold over decades. For instance, the long-lived trees and limited seed dispersal mean that forest communities may require centuries to complete demographic turnover, whereas contemporary anthropogenic warming exceeds historical natural variability, resulting in marked lags between climatic forcing and forest response (Fastovich et al., 2025). Consequently, the informational value of biodiversity data increases exponentially with the length of time series (Robinson et al., 2005). Nevertheless, sustained biodiversity monitoring has been documented as a high-cost endeavor, with cumulative expenditures reaching the millions to billions of dollars—an issue repeatedly identified as a critical financing challenge in recent international assessments (CBD, 2024; NPWS, 2021; UNEP-MAP, 2022).

4 Reconfiguration of the network of PAs at landscape scale

4.1 Expanding the scope of PAs

The establishment of PAs continues to be the best strategy for biodiversity conservation at the global level (Bruner et al., 2001), enhancing species' adaptive capacity. According to the IUCN (2018), the global PA network comprises 238,563 sites, covering 14.9% of terrestrial and 7.3% of marine areas (Elise et al., 2018). The advantages of PAs are that they effectively enrich baseline species diversity, achieve conservation targets, promote population connectivity, and maintain genetic adaptive potential. Expanding the scope of PAs and enhancing habitat quality will enhance the ability of species to adapt to climate change in their original habitat, especially amidst increasingly frequent extreme weather events (Abernathy et al., 2019). The CBD's Aichi Target 11 explicitly incorporates PA coverage in Key Biodiversity Areas (KBAs) as a progress indicator (CBD, 2011). Climate-informed PA expansion requires five strategic considerations.

- (a) Focusing on potential changes in biodiversity distribution under climate change to fill gaps. Species currently outside PA networks, particularly rare and endemic species, should receive priority protection (Rodrigues et al., 2004). Concurrently, restoring ecosystem function requires focusing on gap species' roles in reestablishing the “top carnivore-herbivore-primary producer” trophic network.

- (b) Planning PAs requires considering both replication and representation. Replication entails protecting multiple samples of the same type of ecosystem or population needs to be protected in different areas; when one area is climate-affected, surviving populations in other areas can serve as reintroduction sources (Mawdsley et al., 2009). Representation involves protecting a comprehensive portfolio of PAs, such as the protection of multiple genetically variable populations of a species, different communities of an ecosystem type or multiple habitats (Giraud and Arzamendia, 2017). A key challenge is identifying representative PAs given climate-induced ecosystem transformations and novel species assemblages.
- (c) Prioritization should target areas with greater geographic and climatic diversity (S. Liu et al., 2025). Based on the principle of being the most species-rich and the most threatened, the 34 global biodiversity hotspots—covering merely 2.3% of land area but containing more than 75% of endangered mammals, birds and amphibians—demand urgent protection (Sgrò et al., 2011). Moreover, genetic diversity hotspots should also receive enhanced attention (Schmidt et al., 2024).
- (d) Fully utilizing the conservation value of keystone species, indicator species, pioneer species, umbrella species and flagship species. As Chinese Academy of Sciences Academician Li Zhensheng observed, a single gene can influence the rise and fall of a nation, a single species can shape the economic lifeline of a country, and healthy ecological community can improve regional environment (CAS, 2013). The presence and abundance of these species can have a major impact on ecosystems, and if lost, a ‘butterfly effect’ of change throughout the ecosystem can be triggered.
- (e) Selecting genotype-specific habitats for PA designation to promote *in situ* evolution of species (Dunlop and Brown, 2008), such as areas of steep ecological gradients, areas with recent significant geological or climatic changes (Cowling and Pressey, 2001), including island ecosystems (Cartwright, 2019).

4.2 Restoring landscape connectivity

4.2.1 Structural approaches to connectivity enhancement

In most cases, continuous and intact native habitats are the best solution for biodiversity conservation. However, in reality, a large number of economically or socially significant land-use types have separated PAs into ecological islands. Reconfiguring PA networks can help populations move along ecological corridors and increase population size, thus increasing adaptive resilience and improving resistance to climate change impacts. Corridors, stepping stones and matrices collectively transform scattered PAs into an interconnected network that retains a natural vegetation-like structure, forming PA networks. Linear corridors directly connect PAs through habitat patches of habitat, facilitating species dispersal (Stralberg et al., 2020b). For example, the tri-national Great Limpopo Transfrontier Conservation Area (GLTFCA) elephant-movement corridor network, completed in 2024 by South Africa, Mozambique, and Zimbabwe, provides approximately 15,000 African elephants and wildebeest with 3,500 km² of continuous dry-season migration habitat (Bakari, 2025). Appropriately sized stepping stone patches shorten the spatial distance

between suitable habitats and lower the energetic cost of cross-landscape movement (Schüßler et al., 2020). In the Atlantic Forest of Brazil, the Portal de Paranapanema restoration project established 90 agroforestry stepping stones (5–20 ha each) that reconnected forest fragments, restoring 1,800 ha of contiguous forest within a decade (Hilty et al., 2020). As the largest, most homogeneous, and most connected component of the landscape, the matrix plays a pivotal role in mitigating edge effects when its ecological quality is improved (Ruffell et al., 2017). Colombia's Caribbean Ecological Connectivity Initiative converted 1.5 million ha of agricultural matrix (oil palm, pasture, and urban zones) into multifunctional sustainable-use zones through zonation, integrating them with core reserves and corridors to prevent protected-area isolation (FAO and UNEP, 2020).

Corridors and stepping stones constitute essential supplements to the matrix, offering structural guarantees for species movement and the continuity of key ecological processes. However, it must be noted that:

- (a) Corridor effectiveness is highly contingent upon the dispersal capacity of the focal taxa: volant birds may benefit, whereas amphibians and invertebrates often fail to use corridors that are too narrow or environmentally unsuitable. Lynch (2019) observed that contemporary urban greenway designs disproportionately cater to mammals and birds, neglecting the requirements of low-mobility species (Lynch, 2019). Moreover, Linear corridors are prone to induce edge effects, leading to abrupt changes in microenvironment parameters such as light and wind speed, and may become a diffusion pathway for invasive species (Bennett and Bennett, 2003). In experimental corridors at Savannah River Site, South Carolina, increased edge illumination significantly elevated densities of the invasive fire ant (*Solenopsis invicta*), resulting in a marked decline in native ant diversity (Resasco et al., 2023).
- (b) The successful implementation of stepping stones strategies hinges on critical thresholds of patch area and inter-patch distance, and static configurations may prove inadequate under climate-driven range shifts (Huntley et al., 2008). Saura et al. (2014) argue that stepping stones must attain sufficient area or quality to yield conservation benefits (Saura et al., 2014). Empirical work on the Tianshan Mountains further demonstrated that stepping stones design parameters (size, placement, and species composition) should be dynamically adjusted to match focal species' dispersal distances (Han et al., 2022).
- (c) Matrix strategies confront multiple challenges: heterogeneity management complexity, socio-economic conflicts, and differential species responses. In Queensland, Australia, despite subsidies encouraging pastoralists to retain native vegetation, the economic appeal of high-return crops such as sugarcane has hindered effective heterogeneity management, and avian community structure has shown no significant improvement (Macinnis-Ng, 2014). Whether landscape connectivity restoration enhances biodiversity resilience to climate change depends on the coupled effects of climate velocity, habitat quantity and configuration, landscape fragmentation, the overall extent and elevational gradients of corridors–stepping stones–matrix, and species dispersal capacity. Consequently, dynamically adjusting the spatial extents and areas of corridors,

stepping stones, and the matrix in accordance with climate-change scenarios and species dispersal traits has become the central challenge in contemporary landscape connectivity restoration.

4.2.2 Implementation frameworks and global applications

Research and practice in restoring landscape connectivity can be divided into two categories: focal species-based and network structure-based approaches.

- (a) Focal species-based connectivity, the more traditional approach, involves planning by predicting species' future distribution based on their exposure, sensitivity, and resilience under climate change (Krosby et al., 2015). Key applications include: (i) finding habitats or corridors that will remain valuable for certain priority species even under climate change (Fan et al., 2017); (ii) predicting species distributions based on climate change, and thus determining how to protect area or promote landscape connectivity (Choe et al., 2017). Published researches have also shown passionate concerns about ecological corridor planning for flagship species such as Asian elephants and giant pandas (Mandal and Das Chatterjee, 2023).
- (b) Network structure-based enhances landscape permeability by enriching the physical elements to facilitate species adaptation (Keeley et al., 2018). The specific methods can be summarized as follows: (i) Take advantage of the innate connectivity of waterways (Krosby et al., 2014); (ii) Mapping of environmental gradients based on macro-climatic gradients or land cover permeability (Rouget et al., 2006); (iii) Priority is given to the most natural areas with less human disturbance as corridors (Belote et al., 2016); (v) Design lattice-work corridor along latitudinal/longitudinal axes (Townsend and Masters, 2015); (iv) Maximize the continuity and diversity of the physical environment adjacent to the corridor (Beier and Brost, 2010).

Restoring landscape connectivity based on network structures has been incorporated into biodiversity conservation in multiple countries. Since 1992, to ensure ecological connectivity and habitat quality, The EU's Natura 2000 network (established in 1992) covers nearly 28,000 sites (18% of land area), which is at the heart of the EU's ecological conservation and climate change adaptation program (BISE, 2022). Mitigation banks in the U.A. adopt a range of strategies to conserve, manage and restore degraded habitats, connect fragmented habitats, create buffers and habitats for adaptive conservation of biodiversity (EPA, 2002). The Cape Floristic region of South Africa has a protected area plan that incorporates river corridors across mountains (Pressey et al., 2007). Australia has initiated large-scale landscape restoration and connectivity projects to combat climate change (Taylor and Figgis, 2007). In addition, countries have been developing green infrastructures to restore the connectivity between cities and nature. Green infrastructure is defined as an interconnected network of natural areas (e.g., rivers, wetlands, forests and wildlife habitats), and human-made environments (e.g., green spaces, parks, farmlands and pastures) (Canzonieri et al., 2007), the connectivity of which is essential for the survival of natural species, air and water quality, and human health and quality of life. In 2022, the EU launched biodiversity strategy for 2030, which designated "the

improvement and restoration of ecosystems and their services through the development of green infrastructure” as one of its six headline targets (EU, 2022).

4.3 Identifying climate change refugia

4.3.1 Conceptual foundations and ecological significance

Escalating frequency, intensity, and duration of extreme climatic events impose substantial physiological and demographic stress on biota (Murali et al., 2023). Climate change refugia emerge as pivotal sanctuaries for species persistence and population recovery. Unlike landscape connectivity initiatives that design migration pathways based on species traits and dispersal capacity, refugia-oriented strategies focus on safeguarding residual populations to maintain genetic diversity (Ackerly et al., 2020). Refugia are defined as spatial habitats into which populations contract when confronted with climatic stress, providing critical buffering when necessary (Morelli et al., 2020). For taxa constrained within such refugia, migration or dispersal to more suitable habitats is often precluded by intrinsic or extrinsic barriers (Poulos et al., 2013). Consequently, facilitating population persistence within refugia is pivotal for both post-extinction recolonization and long-term adaptation under climate change, rendering the identification of refugia a priority for biodiversity conservation planning.

Refugia are species- and stressor-specific, shaped by the dynamic interplay between stressors and organisms (Greiser et al., 2020; Stewart, 2010).

- (a) Climate change as the dominant stressor. The velocity and magnitude of climatic shifts constitute the primary criteria for refugium identification (Szcodronski et al., 2024). If global warming is constrained to 2 °C, integrating climate-change refugia into an expanded protected-area network remains feasible (Saunders et al., 2023). For example, the U.S. National Park Service designated the meadow complex of Devils Postpile National Monument as a climate-change refugium and implemented invasive-tree removal to preserve its ecological function (Morelli et al., 2016). When warming exceeds 2 °C, however, most refugia will be restricted to high latitudes and elevations (Lawler et al., 2020).
- (b) Anthropogenic co-stressors. Intensive infrastructure development, habitat conversion and degradation, poaching, and pollution—are critical co-stressors. Contemporary refugia such as nearshore coral reefs of the Great Barrier Reef show reduced survival potential due to land-based runoff driven by human activities (van Woesik, 2025).
- (c) Stressor interactions. The compatibility between landscape attributes and the biophysical thresholds of refugial species is therefore essential (Keppel et al., 2024). Topography, soil type, ecosystem engineers (e.g., beavers), and microclimate modifiers (e.g., forest canopies) facilitate the formation and maintenance of climate-change refugia (Cartwright and Johnson, 2018; Frei et al., 2023; Kuntzemann et al., 2023; Stralberg et al., 2020a). Biophysical thresholds of refugial species serve as key indicators of whether a refugium effectively buffers ecosystems from climate change

(Beaumont et al., 2019; Greiser et al., 2020). For instance, peat-forming bryophytes sustain hydrological feedback that maintains soil moisture, locally reducing fire and drought frequency and thereby promoting refugium formation; conversely, partial drainage or intensified drought reduces moisture retention; once critical biophysical thresholds are exceeded, the buffering capacity of climate-change refugia declines (Kuntzemann et al., 2023).

4.3.2 Technical challenges and uncertainties

Technically, climate change refuge identification depends on the accumulation of data across multiple species, such as relying on phylogenetic comparisons (Keppel et al., 2018), phylogenetic diversity metrics (Costion et al., 2015) and phylogenetic geographical analysis (Liu et al., 2025) to collect genomic data of certain species. Based on the collected species data, SDM is used for large-scale identification. Specifically, the habitat requirements, population dynamics and dispersal of a species are incorporated into bioclimatic models to predict the potential future distribution of a species at local, regional or larger spatial scales, and to identify refuge locations based on current distribution versus modelled future distribution projections (Briscoe et al., 2016). However, refugium identification confronts significant methodological, data and ecological challenges due to the complex interactions among diverse stressors, landscape contexts and refugial taxa.

- (a) Uncertainty in climate models. SDMs serve as a critical tool for identifying refugia (Georges et al., 2024), yet most models primarily correlate species distributions with macroclimatic variables, failing to comprehensively incorporate key ecological factors such as soil properties, vegetation structure, hydrology, land use, invasive species, and behavioral buffering. When projecting future ranges and identifying refugia, due to truncating all acceptable conditions for species, it may encounter niche truncation challenges (Anselmetto et al., 2025), which may either over or underestimate the true location of refugia. Furthermore, SDMs exhibit delayed responses to dynamic changes. Most current approaches rely on steady-state climate assumptions, rendering them inadequate for capturing the immediate impacts of extreme events (e.g., wildfires, droughts) on refugia. For instance, studies on post-glacial oak refugia demonstrate that species migration is strongly climate-driven (Hao et al., 2023), yet existing models struggle to integrate abrupt disturbances (e.g., flash droughts) that may disrupt refugial habitats.
- (b) Limitations in data acquisition across spatial and temporal scales. Data deficiencies create both taxonomic and spatial blind spots in refugia identification. Phylogenetic analyses and genetic diversity assessments rely heavily on existing genomic datasets, yet endangered species frequently lack such genetic information, compromising refugia prioritization. For instance, rare tropical rainforest plants often remain genomically uncharacterized, hindering accurate evaluation of their refugial potential (Costion et al., 2015). Similarly, the Refugia of endemic Pacific island birds have not been included in conservation plans due to genomic data gaps (Sherley, 2001).

Spatial blind spots emerge from reliance on high-resolution environmental data. Refugia identification proves particularly sensitive to spatial resolution and thermal buffering thresholds. Coarse-scale

global climate datasets (e.g., 1-km resolution) systematically underestimate fine-scale temperature variations in topographically complex terrain, causing omission of critical microrefugia (e.g., ravines, caves) (Rosauer et al., 2013). Furthermore, the paucity of high-resolution environmental data in tropical, deep-sea, and polar regions biases identification efforts toward well-studied areas, leaving many potential refugia undetected (Morelli et al., 2020).

- (a) Stressor-species interaction gaps. Most studies focus on flagship species while neglecting community-level interaction dynamics, including competitive interactions among plant species, plant-animal relationships (herbivory, pollination, seed dispersal) (Ackerly et al., 2020); anthropogenic pressures (e.g., trawling impacts on marine refugia, deep-sea mining effects) (Zelli et al., 2025). Climate-human pressure interactions may drive species reassembly and loss, potentially altering ecosystem functioning and potentially unbalancing refugium network design (González-Trujillo et al., 2024).
- (b) Dynamic threshold uncertainty. Microclimatic stability thresholds differ among refugial species and even among life-history stages within the same species, yet these biological thresholds often defy clear identification (Hillebrand et al., 2020) and quantitative characterization (Groffman et al., 2006). Critical knowledge gaps persist regarding the biological threshold at which refugial processes lose their buffering capacity against climate change impacts (Costa et al., 2022).

5 Site scale emphasis on species

5.1 *In situ* and ex situ conservation for keystone species

In 2023, the IUCN released its latest Red List of Threatened Species, assessing 157,190 species, of which 44,016 are threatened with extinction (IUCN, 2023), highlighting the urgency. *In situ* conservation is one of the most effective methods for promoting the population recovery of keystone species, yet accelerating climate change has caused protected-area boundaries increasingly to misalign with shifting climatic envelopes, producing a pronounced spatio-temporal mismatch (IPCC, 2022). The first global assessment revealed that, among 11,633 terrestrial vertebrate species examined, 1,424 (12.2%) are unprotected gap species (Rodrigues et al., 2004), thus necessitating ex situ measures as a supplement. While ex situ measures can immediately avert acute threats for species unable to persist on site, they often do so at the expense of ecological context and evolutionary feedback (Minteer, 2014; Seddon et al., 2014). Integrating dynamic *in situ* management with ex-situ interventions to create a “parallel *situ* conservation” may mitigate mismatch risk while preserving ecological integrity (Feng et al., 2023).

5.1.1 *In situ* conservation for keystone species is the optimal choice

For keystone species, *in situ* conservation is one of the most effective ways to reduce the biodiversity loss on a global scale. The specific implementation is divided into three steps:

- (a) Using data on species richness, endemism, species threatened, taxonomic distinctiveness and habitat uniqueness to varying

degrees to identify keystone species based on vulnerability and irreplaceability (Cottee-Jones and Whittaker, 2012).

- (b) Identifying KBAs on the basis of the previous step and four criteria: threatened species and ecosystem types, geographically restricted biodiversity, ecological integrity, and biological processes (Langhammer, 2007).
- (c) Ultimately, gradually implementing *in situ* conservation programs for different types of KBAs, such as biodiversity hotspots, plant diversity centers, endemic bird areas, and most valuable ecological areas (Bonn et al., 2002).

Thanks to international efforts, 14% of forests (Schmitt et al., 2009) and 88% of vertebrate species (Rodrigues et al., 2004) have been protected in 34 biodiversity hotspots around the world, and *in situ* conservation of species has been actively promoted. However, half of the world's KBAs are still unprotected (Butchart et al., 2012). In addition, *in situ* conservation on the site scale has difficulty maintaining good ecological processes because of inadequate management effectiveness and the isolation of PAs from each other, and the loss of biodiversity at the population level is often prone to far-reaching ecological and evolutionary consequences, such as the loss of top predators. Under land use pressure, *in situ* conservation faces the enormous challenges of feeding 9 billion people by 2050 and biodiversity conservation.

5.1.2 Ex situ conservation aids retention of endangered species

Endangered species are more susceptible to climate change and there are climate thresholds beyond which the probability of extinction increases dramatically, thus making ex situ conservation an important initiative for the adaptive management of endangered species (Solomon et al., 2007). Ex situ conservation refers to the relocation of plants, animals and other organisms from areas that have become unsuitable to other areas that are suitable for survival in form of assisted dispersal (Liu et al., 2014), assisted migration (Guinan et al., 2025) and assisted colonization (Gallagher et al., 2015). Ex situ conservation requires three criteria to be met: (i) Seed to seed, requiring relocated plants and animals to be able to grow freely and survive through sexual reproduction; (ii) Representation requires that relocated species maintain genetic integrity and represent the genetic diversity of the population; (iii) Maintaining the population gene frequencies of genes after translocation to avoid outbreeding depression, genetic assimilation and introgression (Engelmann and Engels, 2002; Quinlan et al., 2025). Targets 12 and 13 of the Aichi Biodiversity Targets call for the conservation of biological genetic diversity through ex situ conservation projects (Geijzendorffer et al., 2017), and countries around the world are actively exploring ex situ conservation systems, which have been extended to cover wildlife, crops, domesticated animals and microbial strains.

While significant achievements have been made in ex situ conservation, it is crucial to recognize its distinctive characteristics. (i) Unlike climate change refugia that emphasize population relocation and long-term retention in natural systems, ex situ conservation focuses on species under human intervention. For example, wild plant conservation primarily utilizes botanical gardens and seed banks; food and agricultural plant preservation employs germplasm repositories and nurseries; wild animal conservation relies on zoos, safari parks, aquaria, and other captive breeding programs; while microbial conservation is accomplished through strain conservation (FAO, 2007). (ii) Ex situ conservation

attempts may fail and even accelerate species extinction. A tragic example is the 1981 capture and captive breeding of Japan's last five crested ibises (*Nipponia nippon*), which ultimately failed to prevent the species' extinction in 2003 (Biodiversity Center of Japan, 2024). (iii) Under climate change scenarios, ecosystem transformations may become so profound that species reintroduction becomes unfeasible, potentially turning ex situ conserved populations into evolutionary relicts (Minteer, 2014). (iv) Technical constraints include: (a) climate model uncertainty and error may cause mis-translocation risk, as evidenced by the Poweshiek skipperling (*Oarisma poweshiek*) conservation program in the U. S., where climate model biases led to dramatic post-release survival declines (Runquist et al., 2025); (b) small population sampling reduces genetic diversity (Mclachlan et al., 2007). A global meta-analysis confirmed that inadequate wild population sampling resulted in significantly lower genetic diversity in restored populations compared to reference groups over 50 years, impairing long-term adaptive capacity (Wei et al., 2023); (c) microhabitat mismatches increase post-release mortality; and (d) translocated individuals can introduce or encounter novel pathogens. In Canada, the ex situ conservation of whitebark pine (*Pinus albicaulis*) faced dual threats: the absence of Clark's nutcracker (*Nucifraga columbiana*), its natural seed disperser in native habitats, and the concurrent spread of white pine blister rust (*Cronartium ribicola*) to recipient sites (Sáenz-Romero et al., 2021).

5.2 Monitoring invasive alien species

Climate change is a pivotal factor in the acceleration of invasive species incursions (Liu et al., 2017). Throughout the sequential process of biological invasions, the repercussions of climate change can emerge at various stages. To begin with, the warming climate may expedite the developmental pace and amplify the reproductive cycles of invasive species. Following this, climate change has the potential to reshape the distribution and the spatial extent of an organism's impact. Ultimately, the warming trend could augment the phenological flexibility, competitive prowess among species, and the growth-defense trade-offs of invasive flora, thereby disrupting the intricate relationships between hosts, pests, and predators (Gu et al., 2023). The encroachment of alien species, further perturbs biogeographical distributions, impinges on the diversity and genetic integrity of native species, and escalates the peril of extinction for indigenous taxa. It is estimated that invasive alien species and their management cost the global economy billions of dollars annually (IUCN, 2018). The Strategic Plan for Biodiversity (2011–2020) requires Parties to take urgent action to identify and prioritize invasive alien species pathways to prevent their introduction and rooting (CBD, 2015). To achieve these goals, the following aspects must be taken into account:

- (a) Border controls are the first barrier. Biosecurity mechanisms must be established at the national level to regulate intentional introductions, use technology to mitigate the effects of unintentional introductions, and encourage community participation in monitoring and managing invasive alien species. Almost all countries have introduced regulatory provisions related to invasive alien species based on risk assessment, establishing strict quarantine controls at borders to prohibit the import and trade of regulated species; or using a white-listing approach to prohibit the introduction of all

nonnative species unless they are determined to be low risk (Genovesi et al., 2015).

- (b) Once invasive alien species have already invaded the region, eradication or impact mitigation must be pursued through conventional control, gene editing and other methods. Conventional control including physical control (Leary et al., 2013), chemical control (Simberloff et al., 2018) and biological control (Veitch et al., 2019). In the last decade, gene editing techniques have been progressively introduced, such as gene silencing, where specific genes of invasive species are not expressed or are not significantly expressed to reduce their spread (Martinez et al., 2020). Gene editing techniques are often used in combination with transgenesis and, while they can help to manage or eradicate of invasive alien species, their potential unintended consequences need to be addressed (Callaway, 2018).
- (c) The involvement of stakeholders from across society is crucial for controlling invasive alien species. Widespread community participation can collect more valuable data on invasive alien species. For example, people can readily identify and record invasive alien species through mobile phones and apps, which not only further increases their awareness of biosecurity and early monitoring capabilities, but also helps to record their location and spread pathways.

6 Conclusions and future prospects

6.1 Conclusion

Compared to other anthropogenic environmental threats, climate change will exert more gradual, more difficult-to-quantify, and largely irreversible impacts on biodiversity. Given biodiversity's critical importance to human society and the inherent uncertainties of climate change, developing cross-scale adaptive management strategies is imperative. This paper examines adaptive management strategies to enhance biodiversity resilience under climate change, employing a cross-scale "region-landscape-site" framework. Key findings include:

- (a) Cross-spatial-scale synergy is key to biodiversity adaptation to climate change. This study proposes that multi-scale collaboration across "regional-landscape-site" levels can systematically enhance the adaptive capacity of biodiversity to climate change and reduce its vulnerability. This finding deepens existing adaptation frameworks: whereas Mawdsley et al. (2009) focused on a horizontal classification of action types and Heller and Zavaleta (2009) emphasized the functional aspects of strategies, this study highlights the spatial dimension of vertical integration across scales, thereby extending the theoretical framework. This perspective aligns with insights from case studies such as those in the Andes (Hole et al., 2011) and coastal wetlands (He et al., 2025), which also identify cross-scale coordination as central to effective adaptation. This study further formulates a universal theoretical model, suggesting that scale synergy can address uncertainties associated with climate change through both "ecological cascading" and "governance implementation" dimensions. The primary contribution of this research lies in constructing a

systematic adaptation framework centered on “scale synergy,” moving beyond earlier research paradigms that categorized actions or strategies in isolation. It reveals the inherent connections and interactive mechanisms among multi-scale conservation strategies. This systemic perspective can help policymakers identify scale disconnects during implementation and offers significant theoretical value for the adaptive management of complex ecosystems. However, the practical application of this framework faces several challenges, which also represent limitations of this study. These include scale mismatches between problem identification and governance levels, difficulties in identifying ecological cascades across spatial scales, barriers to vertical policy integration, and delays in adaptive management feedback.

- (b) Biodiversity adaptation strategies at different scales have distinct emphases yet are mutually reinforcing. The regional scale focuses on top-down design and systematic assessment, providing strategic guidance for lower levels through macro-level planning and continuous monitoring. The landscape scale emphasizes spatial restructuring and network optimization—including protected area expansion, connectivity enhancement, and climate refuge identification—to facilitate species movement and persistence. The site scale prioritizes direct interventions targeting key species, such as *in situ*/ex situ conservation and invasive species control, representing the most immediate and concrete conservation actions. Although these strategies are widely recognized, the innovation of this study lies in integrating them into a coherent system with clearly defined hierarchical support relationships, elucidating the interdependencies among strategies across scales. For instance, species conservation at the site scale relies on landscape connectivity to support successful reintroduction and population recovery, while landscape optimization depends on regional-scale vulnerability assessments and planning prioritization. Together, these three scales form an organic whole: actions at lower levels facilitate the implementation of higher-level strategies, while upper-level planning provides the framework and basis for localized interventions. Nevertheless, integrating multi-scale strategies still faces resource- and knowledge-related barriers, such as: (i) competition for limited conservation funding among strategies operating at different scales, making optimal resource allocation challenging; and (ii) difficulties in effectively integrating site-level monitoring data into landscape and regional scales to support macro-decision-making, coupled with the generally insufficient resolution of regional climate models to provide precise guidance for site-specific management.

6.2 Future prospects

The adaptation of biodiversity to climate change is a long-term, social learning process that requires individuals and societies to increase their awareness of potential future changes and enhance their capacity to cope with them. Future efforts must address critical challenges, including social inequities, lags in dynamic landscape

conservation planning, dynamic imbalances in species' ecological networks, and barriers to interdisciplinary support.

- (a) At the regional scale, policies for biodiversity adaptation confront both domestic and international social inequities. Biodiversity conservation has significant positive externalities. However, biodiversity-rich regions are often less developed regions that face three constraints: development limitations imposed by conservation requirements. High dependence on climate-sensitive sectors (e.g., agriculture), and lack of technical and financial resources to withstand climate change (Marshall et al., 2016). Furthermore, climate change may exacerbate current regional inequalities (Feliciano et al., 2025). Therefore, future policy design and international cooperation must explicitly incorporate equity, fairness, and distributional considerations, evaluating how policies affect balanced regional development, stakeholders responses, and the burden placed on the poor, etc.
- (b) At the landscape scale, response lags in dynamic landscape-conservation planning pose a future challenge. Natural disturbances, succession and climate cycles drive spatial shifts in suitable habitats. Dynamic landscape conservation explicitly addresses biodiversity's climate adaptation needs at this scale, incorporating both structural and functional connectivity responses to environmental change (Xu et al., 2025). By enhancing cross-scale, long-term monitoring, climate impact assessments, and risk analyses, this approach enables prediction of species redistribution and ecosystem transitions, quantification of landscape-level dynamics, and development of proactive conservation targets to guide adaptive management. Regrettably, a major constraint remains: the limited availability of large-scale, high-resolution, long-term ecological datasets essential for reliable implementation.
- (c) At the site scale, dynamic imbalances in species' ecological networks hinder the maintenance of complex ecosystem stability, thereby impeding species adaptation. While flagship species such as the giant panda and Asian elephant attract policy attention and function as umbrella species, the neglect of non-charismatic or lower-trophic-level species can alter matrix ecosystem structure (Poiani et al., 2000), undermine network stability, and erode adaptive capacity. Ecological-network models require actions that explore the links between complexity and stability (Landi et al., 2018), and foster dynamic equilibrium within habitats, thereby promoting species adaptation and sustaining ecosystem services.
- (d) Interdisciplinary support across all three scales remains inadequate. Most existing proposals focus on ecology disciplines, underestimating the contribution of the social sciences. Effective biodiversity adaptation across spatial scales demands large geographical coverage, long time-frames, integration with species-conservation plans, natural resource management, and the livelihoods of local people, etc. (Frison, 2024). Capacity building must therefore be truly multidisciplinary, engaging atmospheric sciences, biology, ecology, geography, agronomy, sociology, economics and management.
- (e) It is imperative to heighten attention to the synergistic impacts of human activities and climate change on biodiversity. Climate change, human activities, and their interactions are the

strongest drivers of biodiversity loss. Although the scientific community has directed significant concern towards climate change (Mazor et al., 2018), it is crucial to acknowledge that human actions, especially those involving excessive development, continue to pose the most significant threat to species at risk as noted in the IUCN Red List (Maxwell et al., 2016). Habitats conversion driven by agricultural expansion, deforestation, marine fishing, and urban sprawl—exacerbated by climate change—constitutes the primary cause of biodiversity decline. The cumulative amplification of multiple stressors can trigger cascading effects, potentially undermining conservation initiatives (Brook et al., 2008). Future research endeavors should concentrate on elucidating the intricate interplay between climate change and human activities in relation to biodiversity, and devising integrated planning and management strategies.

Author contributions

XM: Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization, Visualization, Methodology. LJ: Investigation, Methodology, Writing – original draft. LS: Writing – original draft. ZQ: Project administration, Writing – review & editing, Funding acquisition, Supervision.

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