



Synergies between speciation and conservation science yield novel insights for mitigating the biodiversity crisis of the Anthropocene

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The Earth is experiencing ongoing and devastating environmental change, largely, if not entirely, due to anthropogenic impacts. This is leading inexorably to the fragmentation of our biosphere and threatens biodiversity across all continents and habitats. While forests harbor over 80% of terrestrial biodiversity, 70% of the Earth's remaining forests are within 1 km of a forest edge (1). The loss of aquatic habitat is equally alarming, iconically represented by the dramatic loss of coral reef habitat, which is projected to reach an 84% loss in response to ongoing climate change (2–5). Indeed, the simultaneous impacts of habitat fragmentation and land conversion (6, 7), species loss (8–10), the proliferation of “anthropogenic mass” (11), and, notoriously, climate change (12) are disrupting virtually all natural systems, and with catastrophic consequences (13). The Kunming-Montreal Global Biodiversity COP15 Framework established a global agreement to designate 30% of land as protected areas, which, though promising, still falls short of the 44% of terrestrial habitat that is needed to prevent major biodiversity loss (14). And though biologically informed connectivity among protected areas can increase their ecological efficacy, only ~10% of the global terrestrial protected areas are structurally connected (15, 16) with critical connectivity threatened by land use conversions (17). This accelerating process has served as a call-to-arms for ecologists and evolutionary biologists alike, especially given the need to develop operational guidelines that define a well-connected landscape (18). Here, this Special Feature focuses on the challenges of measuring, monitoring, and maintaining the exchange of genetic material among wildlife populations (i.e., “gene flow”) as a means for restoring connectivity in an increasingly fragmented world (17, 19).

Like several other recently published Special Features (20–27), this collection of papers is devoted to exploring the applications of basic science for mitigating challenges to biodiversity that result from a human-modified and fragmented landscape. The eleven papers in this collection coalesce around the goal of conserving species and their ecosystems by examining the role of gene flow among organismal populations and its fundamental relationship to landscape connectivity. The collection pursues this goal by linking the traditionally distinct scientific agendas of speciation and conservation biology, focusing on how this collaboration can translate to conservation innovation and application. Though they might at first appear to be paradoxically opposed, with speciation biology focused on the origin of species due to cessation of gene flow, and conservation science focused on preventing the extinction of species by the promotion of gene flow, this collection of papers highlights their conceptual continuity across the speciation-extinction continuum (Fig. 1).

The papers in this collection synthesize advanced methods, empirical ecological genomic research, nature-informed conservation policy, and innovative infrastructures for assuring the persistence of gene flow in the fragmented ecosystems of the Anthropocene. We have invited scientists across a broad range of basic and applied scientific disciplines to explore the connections between basic biodiversity research and its applications to conservation action (Table 1). The topics covered represent a spectrum of approaches, ranging from the theoretical to the applied, and take the reader through cutting-edge methods for modeling and elucidating patterns of gene flow in a variety of organismal systems where gene flow has either naturally or artificially reshaped evolutionary trajectories. The collection concludes with astute perspectives on conservation methods and strategies that situate biodiversity conservation within the socioeconomic realities of a human-modified landscape.

Habitat Fragmentation and the Extinction Vortex

The term Anthropocene was originally coined for the period of Earth's history coincident with the rising carbon dioxide and methane levels caused by the Industrial Revolution (39). Though the term has been controversial (40) and was ultimately rejected by the International Union of Geological Sciences (IUGS) in March 2024, the IUGS nonetheless noted that “The Anthropocene as a concept will continue to be widely used not only by Earth and environmental scientists, but also by social scientists, politicians and economists, as well as by the public at large. As such, it will remain an invaluable descriptor in human–environment interactions.” In effect, the Anthropocene has become shorthand for “overwhelming environmental change” due to anthropogenic causes (41), and it is in this context that we use it here.

From the earliest days of the modern evolutionary synthesis, theorists recognized that in small populations there

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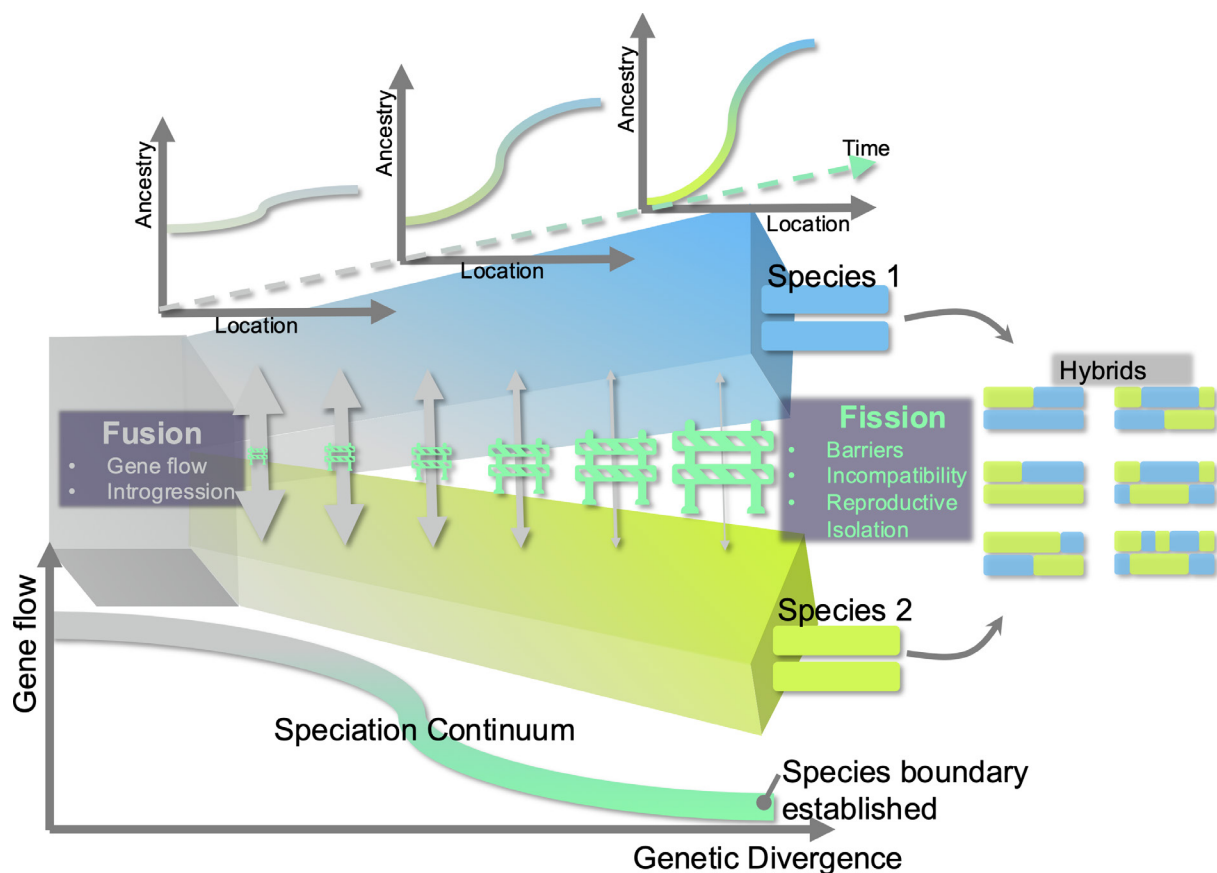


Fig. 1. A conceptual model of fusion and fission in the Speciation Continuum can empower conservation biology. As geographic barriers (fission) accumulate to prevent gene flow (fusion) between diverging lineages, they become increasingly diverged, ultimately leading to speciation via reproductive isolation. The process is complete with the cessation of hybridization in sympatry or when hybrids are either inviable or drastically less fit than parental lineages. While gene flow promotes fusion, habitat fragmentation drives fission. Conservation science strives to understand the population consequences of isolation (fission) and mechanisms for restoring gene flow (fusion) over fragmented habitats. Speciation and conservation science are conceptually centered around this tension between fission and fusion.

is an increased probability that genetic relatives will interbreed, yielding offspring with genomes that contain an overabundance of alleles that are identical by descent (IBD). Under these conditions, and with increasing numbers of generations through time, offspring will be produced with abnormally high levels of homozygosity and an overexpression of recessive alleles largely due to IBD. Ultimately, these descendant populations will lose genetic variation via reduced heterozygosity and the accumulation of deleterious alleles – a condition that is referred to as “genetic load” due to inbreeding depression (42–47). Drawing from this classic population-genetic theory, it can be argued that the “extinction vortex” model marks the origin of modern conservation biology (48, 49). This model provides a framework that integrates ecological, demographic, and population genetic elements as necessary for predicting population extinctions in the face of anthropogenic environmental change. It defines positive feedback loops where the decay of one factor (e.g., population size) exacerbates a death spiral wherein shrinking habitats drive population declines, leading to loss of genetic diversity via inbreeding, and ultimately, reduction in fitness and evolutionary potential – a reinforcing loop that inexorably leads to population extinction.

The damaging consequences of population isolation via anthropogenic habitat fragmentation is powerfully illustrated

in a now classic study that compiled thirty-five years of natural experiments across multiple biomes and continents (1). That study found that habitat fragmentation consistently negatively impacted species richness, community composition, and ecosystem function. The study also hypothesized that fragmentation can have delayed impacts that lead to “extinction debt,” wherein species loss is delayed or prolonged, “immigration lag,” wherein species accumulation is compromised, and “ecosystem function debt,” wherein detrimental changes to ecosystem function are not immediately measurable. Early conservation genetic studies concluded that there is “an urgent need for conservation and restoration measures to improve landscape connectivity” (50, 51). Thus, the field of conservation biology has increasingly focused on strategies for enhancing connectivity and gene flow across the landscape (52–54).

Subsequently, empirical studies have been conducted to more directly examine organismal fitness in degraded habitats that interfere with or truncate previously continuous gene flow (42, 46). Evidence from natural populations is rapidly mounting, showing that the loss of heterozygosity leads to deleterious impacts on fitness such as reduced birth weights (in vertebrates), lowered probability of survival, lowered reproductive output, and diminished disease resistance (55). Moreover, these impacts can be seen across a broad

Table 1. Terminology and conceptual synergies between speciation and conservation biology with connections to papers in this special feature

Speciation biology	Conservation biology	Conceptual connection	Relevant papers within this special feature
Populations	Species	The biological unit of greatest interest within the evolutionary continuum	van der Heijden et al (28); Tobias et al. (29); Ellis-Soto et al. (30)
Effective population size (Ne)	Sustainable population	The number of individuals necessary for population persistence and/or growth	Zhu et al. (31); Naidoo et al. (32)
Adaptation	Reproductive potential	Populations with healthy levels of genetic diversity are more likely to persist in changing environments by producing offspring that carry adaptive alleles	Owens et al. (33); Massatti et al. (34); Tobias et al. (29)
Bottleneck	Inbreeding	Lack of genetic exchange can result in populations wherein individuals accumulate excess levels of homozygosity	Aguilar-Gómez et al. (35); Lewanski et al. (36); Sgarlata et al. (37)
Expansion load, migration load, mutation load, outcrossing load vs inbreeding load	Genetic load	Individuals with an excess of recessive and maladaptive alleles due to mutation, inbreeding, outcrossing, migration, or population expansion.	Aguilar-Gómez et al. (35)
Admixture/hybridization	Gene flow	Genetic exchange between populations can improve fitness by introducing and maintaining genetic diversity	Zhu et al. (31); Aguilar-Gómez et al. (35); Lewanski et al. (36); Owens et al. (33); Massatti et al. (34); van der Heijden et al. (28); Sgarlata et al. (37); Kong et al. (38); Naidoo et al. (32)
Adaptive introgression	Genetic Rescue by translocation	The introduction of adaptive genetic diversity either by natural or artificial means	Aguilar-Gómez et al. (35); Lewanski et al. (36); Owens et al. (33); Kong et al. (38)
Movement ecology	Biodiversity corridors	The study of organismal immigration and emigration in the context of environmental/habitat structure	Zhu et al. (31); Sgarlata et al. (37); Tobias et al. (29); Ellis-Soto et al. (30); Naidoo et al. (32)

Authors were asked to self-select up to three conceptual categories.

phylogenetic spectrum (56), demonstrating that populations that reach a critical genetic load lose resilience to environmental stress and are therefore prone to extinction (57).

An oversimplified view of inbreeding depression can be argued, however, to ignore fundamental demographic factors that may either be predisposing or, alternatively, resistant to extinction (58). These include factors like life history variation, dispersal abilities, and social structure. For example, long-lived large-bodied organisms with long generation times may be less resilient to environmental perturbations than organisms with short generation times and rapid population turnover (59). Consequently, demography can ultimately play an immediate role in determining the minimum viable population size for evolutionary persistence in the face of severe habitat destruction and thus plays a critical role in determining the likelihood of extinction for small and isolated populations (60). Thus, a fully informed perspective on extinction risk following habitat fragmentation will consider both genetic and demographic risk factors.

Restorative Insights from Speciation Biology

Speciation research is ideally suited to offer this perspective. Rooted in the interplay between organismal gene flow (fusion) and reproductive isolation (fission), lessons learned from decades of speciation research offer an ideal framework for monitoring population connectivity via gene flow over space and time. The speciation literature harbors concepts and approaches for understanding adaptations underlying lineage

divergence (61–65), monitoring gene flow among diverging populations and species (66–69), and for measuring genetic diversity in populations of interest (70–72). Drawing from the geographic modes of allopatric, peripatric, and parapatric speciation (Fig. 2), we can develop process-oriented conservation programs that balance fusion and fission to restore ecosystem integrity. The three modes span a continuum of geographic scales from instances where two populations progress to species differentiation when an ancestral population is severed for an extended period of time into two (or more) lineages by physical isolation (allopatric speciation) (Fig. 2A) (73–75), to a small population that is physically isolated from a source population (peripatric speciation) (Fig. 2B) (76), or finally, to scales where populations are gradually and spatially isolated from a distant source population (parapatric speciation) (Fig. 2C) (77, 78). In each of these scenarios, it is theorized that barriers to reproduction accumulate through genetic drift or directional selection (or both), ultimately transitioning from “fusion” (gene flow) to “fission” (isolation). These processes are thus conceptually applicable to anthropogenic land use changes that result in the geographic isolation of global biodiversity via habitat fragmentation (Fig. 3).

These insights counter the common misconception that speciation research is limited to the latest stages of reproductive isolation when speciation can be considered complete, implying that it is not applicable for anthropogenic isolation that is occurring on shorter timescales. In fact, speciation research studies ecoevolutionary forces across the “Speciation Continuum” (79–81), from the onset of lineage

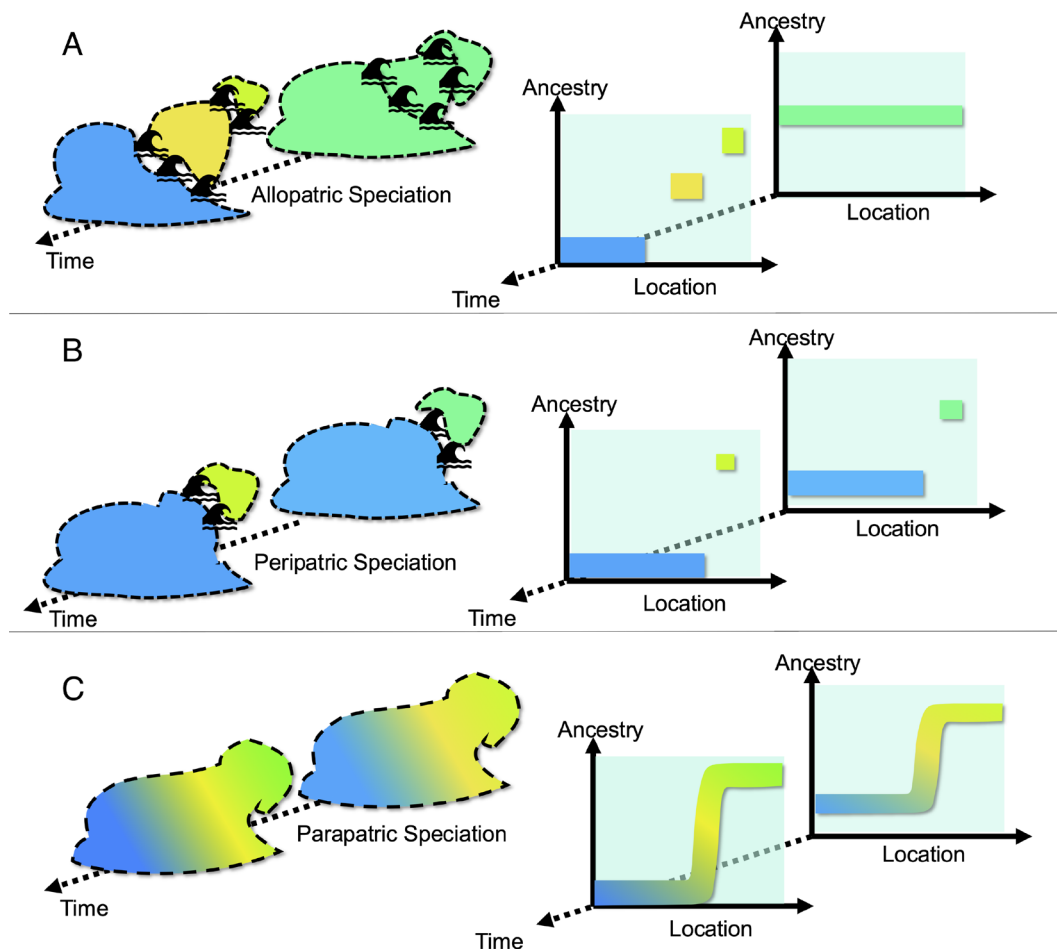


Fig. 2. Three classic models of geographic speciation are increasingly relevant for understanding the impacts of habitat fragmentation on natural populations in an increasingly fragmented landscape. (A) allopatric, (B) peripatric, and (C) parapatric models of speciation.

divergence among populations, with few genetic barriers to gene flow, all the way to genome-wide barriers and the completion of reproductive isolation and/or hybrid sterility. With the advancement of genomic methods and increased sophistication of coalescent theory, gene flow has been increasingly disclosed as more common during the speciation process than we previously appreciated (82, 83).

The future health of our global ecosystem depends on present speciation rates counteracting extinction rates to maintain species richness while preserving underlying ecological form and function. Speciation rates interact with the species–area relationship (SAR), and thus are predicted to be increasingly impoverished with habitat loss and fragmentation (84). There is a core understanding that the evolutionary tension between fusion (gene flow and introgression) and fission (geographic isolation, incompatibility, and divergent selection) underlies the evolutionary histories of the myriad species that compose our biosphere (80, 85–93). The speciation literature of the past several decades has established a spatial, continuous, and ecological foundation for understanding gene flow (94–100), and via integration with conservation science, can advance the predictability and performance of applied conservation practices.

Decades of island speciation and biogeographic studies have elucidated the relationship between speciation rates and SAR, which has significant implications for biodiversity

conservation in fragmented ecoregions (101–106). For instance, as has been classically demonstrated to sustain species richness in anolis lizards (104), the size of a continuous ecoregion is often positively associated with speciation rates (103, 104, 107) with islands greater than 3,000 km² in area having speciation rates that exceed immigration rates. In turn, species richness is positively associated with diversification rate (108) by buffering extinction risks (109) and increasing speciation rate via competition (110) and niche divergence (111).

To be successful, efforts toward ecosystem management must therefore consider future environmental challenges as they differentially threaten multiple lineages across the tree of life (55, 112–114). Fundamentally, the goal is to incorporate the principles of evolutionary genetics at the population level to inform management strategies (115, 116). For example, many conservation management plans include a focus on preserving and/or creating forest corridors (59, 117) in the context of understanding organismal behaviors and dispersal abilities (118). Proposed strategies consider that both large (119) and small (120) areas of natural habitat should be targeted for protection. With appropriate intervention, networks of habitat can be prioritized as “stepping stones” for dispersal (121), and in dire circumstances, wherein populations are known to be in grave genetic distress, “assisted colonization” (117) or “genetic

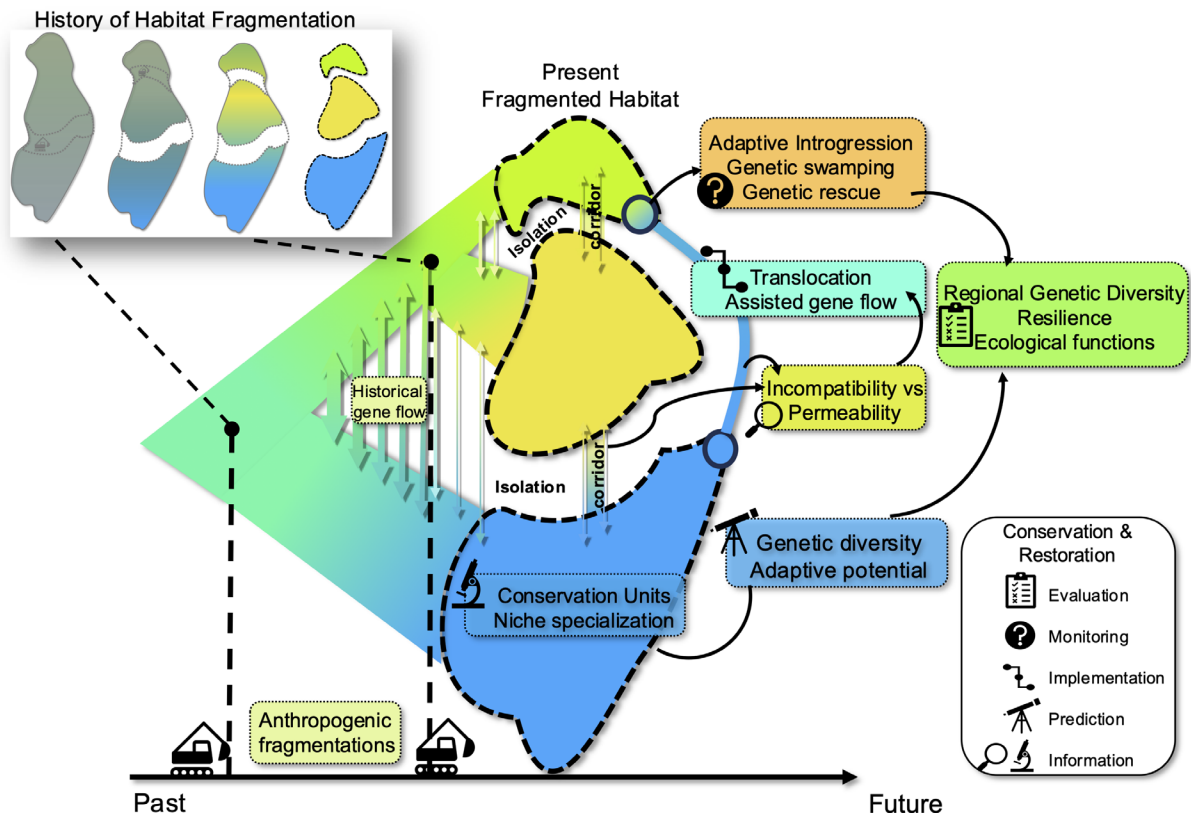


Fig. 3. Process-driven insights from speciation research can empower restoration practice in a rapidly changing and fragmented landscape. Anthropogenic habitat loss imposes isolation analogous to natural allopatric speciation. Concepts and ideas in speciation-introgression research can guide rigorous and effective monitoring of gene flow for planning, prediction, and assessment of functional connectivity in regional restoration efforts.

rescue" can be attempted (122–124). And ultimately, it is critically important to democratize access to advanced technologies and databases in biodiverse developing nations (125)

Adaptive Introgression is Nature's Genetic Rescue

It follows that one of the first tasks for understanding whether a given population may be at extinction risk is to monitor the extent and rhythm of gene flow through its evolutionary history. Thus, we need methods to measure the degree, direction, and timing of natural introgression. Zhu et al. (31) do just that by demonstrating the power of multispecies coalescent methods (MSC) to characterize the extent and direction of gene flow among populations. By examining exon sequences from three species within the genus *Camelus*, their study finds that there has been substantial gene flow from domesticated into a wild species. This coalescent perspective thus informs the common pursuit of "balance" in conservation practices for infusing new genetic diversity from allopatric populations while conserving the background genomic ancestry of the rescued population.

The two subsequent papers in this Special Feature examine the genetic mechanisms and long-term consequences of "genetic rescue" via human-mediated translocation. In the first of the two, Aguilar-Gómez et al. (35) investigate genetic diversity within Florida panthers (*Puma concolor*) nearly thirty years after an iconic effort to rescue inbreeding in the only breeding population of panthers east of the Mississippi River.

In 1995, eight panthers from an allopatric population in Texas were introduced into southern Florida. Subsequently considered to have been a success (126), the mechanisms by which the panthers were "rescued" have until now been obscure. Aguilar-Gómez et al. shed light on the mechanisms of success, finding that the Florida population has experienced an increase in levels of heterozygosity, thus alleviating genetic load, though surprisingly, not via an actual reduction in the number of deleterious variants. Moreover, they find evidence that the ancestral genetic signature of the Florida panther has remained intact, thus alleviating the fear of "genetic swamping." In the second paper to address the subject, Lewanski et al. (36) examine the establishment dynamics and long-term outcomes of a translocation intervention in Red-cockaded Woodpeckers. Analyzing results from more than twenty years of population monitoring, Lewanski et al. find that the project has led to increased population growth, enhanced survival and reproductive success, and, like the findings of Aguilar-Gómez et al., increased levels of heterozygosity. Thus, taken together, these two papers effectively measured the genetic status of endangered populations and quantified the effectiveness of conservation efforts. Both papers offer a beautiful illustration of the ongoing tension between fission (establishment of local ancestry via historical isolation) and fusion (genetic rescue through human-mediated gene flow).

By focusing on the tension between fission (fragmentation, isolation, population bottlenecks, population identity, local adaptation) and fusion (connectivity via gene flow), speciation research has long been monitoring isolation and

connectivity in concert to determine whether and when evolutionary trajectories become independent. Two papers in this collection examine this tension in different empirical systems. Owens et al. (33) delve into a natural occurrence of trans-specific gene flow (i.e., “introgression”) in the sunflower genus *Helianthus*, finding that there has been cytoplasmic introgression across strong reproductive barriers separating species. Finding that two distinctive chloroplast clades differ from the underlying species tree, the authors conclude that chloroplast introgression has brought adaptive advantages for divergent environments to their respective host species. To use the “genetic rescue” metaphor, natural introgression has served to produce enhanced fitness under challenging environmental circumstances. Similarly, Massatti et al. (34) empirically demonstrate that natural hybridization in multiple plant communities in western North America has facilitated niche expansions into novel environments thanks to unique combinations of adaptive genetic variation. Like the Owens et al. study, Massatti et al. conclude that mosaic hybridization can yield adaptive phenotypes that transcend species boundaries. Both studies, therefore, emphasize the importance of introgression as an underappreciated mechanism for conservation innovation.

The Vital Role of Gene Flow in a Fragmented Landscape

Taking from the previous two examples, speciation research can provide dynamic insights into the fluidity of species/population boundaries over time. Geologic forces such as plate tectonics (127, 128) and glacial cycles (65, 129–132) have shaped population isolation, movements, expansions, contractions, and contacts over time, mediating fusion and fission among evolutionary lineages and giving rise to existing global biodiversity. In particular, the Pleistocene epoch, wherein glaciation and other climatic cycles scattered populations and species into isolated refugia to later reconnect and exchange genes, is now considered to be a classic example of a climate-driven “speciation pump” that produced periods of rapid allopatric speciation (133–135). Thus, it is a logical conceptual shift to apply speciation models to the ongoing habitat fragmentation consequent to anthropogenic land use, from agricultural to transportation, and architectural. As natural habitats become increasingly fragmented (1, 136), artificial patterns of allopatry and/or peripatry can arise, placing species at increased risk of extinction as they lose genetic diversity (57, 137). This “anthropogenic allopatry” or peripatry can exhaust speciation potential and compromise future ecological communities (84). By leveraging speciation and introgression insights, conservation biologists can guide effective monitoring, managing, and restoring connectivity via corridors and/or protected areas among fragmented habitats (138) even in the face of socioeconomic complexity (139, 140).

This tension of isolation and gene flow is reflected in the empirical work presented by van der Heijden et al. (28), who find that cycles of isolation and hybridization underlying the radiation of *Melinaea* and *Mechanitis* butterflies were likely driven by these Pleistocene climatic oscillations. The authors hypothesize that repeated periods of geographic isolation established genomic diversity that has been recombined and enriched by gene flow in subsequent secondary contacts.

Such insight links species-oriented delimitation and process-oriented conservation practices.

Along these lines, Sgarlata et al. (37) use spatial simulations to examine the effects of population isolation on genetic diversity. They find that patterns of isolation-by-distance can be maintained for thousands of generations after fragmentation, concluding that these patterns are more strongly influenced by the rate of dispersal than by demographic properties such as population size or mutation rate. This then reinforces the importance of gene flow for shaping genetic diversity after population isolation. In turn, the paper by Kong et al. (38) addresses the obvious questions raised by Sgarlata et al. and van der Heijden et al. – how can we reconstruct the evolutionary history of rapid radiations with gene flow, given that they produce such tangled phylogenomic signals? Emphasizing the point that species must be delimited and described before they can be clearly integrated into conservation management strategies, the authors describe phylogenetic methods that explicitly integrate reticulate evolution into phylogenetic reconstruction. By providing critical details on how phylogenetic networks treat patterns of hybridization and chromosome duplications, Kong et al., emphasize the myriad ways that characterizing reticulate evolution can provide context for interpreting species distributions and patterns of genetic variation thus advancing our ability to monitor gene flow in dynamic and fragmented landscapes.

Biodiversity Conservation via Functionally Connected Landscapes

Though nearly one-sixth of the global terrestrial surface now falls within a protected area (141), urban expansion is expected to lead to as much as 33 million hectares of habitat loss by the year 2100 (142). Many protected areas are underfunded, ecologically damaged, and/or poorly managed (143) and will continue to lose biodiversity if they are isolated by inhospitable human-modified landscapes. Thus, an increasingly obvious solution is to integrate the needs of people into the biodiversity conservation equation (144–146), especially taking into account the growing challenges of a changing climate (147). To assess the effects of human activities on the landscape, one must characterize the defining features of modified landscapes and their consequences for organismal movement (148) (Fig. 4).

Migration monitoring, breeding biology, and fitness have been commonly established in the speciation literature (149–152). But even with these insights, conservation efforts have difficulty stemming biodiversity loss, at least in part because ecosystem functions have largely been measured under current conditions without regard to the anticipated environmental perturbations of the future (i.e., “ecosystem function debt”). This emphasizes the imperative that ecosystem resilience is mandatory for assuring long-term conservation success (153). For example, a recent meta-analysis of 4006 taxa across six continents demonstrates that fragmented landscapes consistently have lower diversity across all measures, clarifying the need to restore and increase both functional and ecological connectivity to maintain biodiversity (154).

Three of the papers in this Special Feature directly address this translational power of evolutionary and ecological knowledge for guiding conservation action. Tobias et al. (29) set



Fig. 4. Process-oriented conservation centered around the tension between fusion and fission can effectively unite species-oriented and process-oriented conservation efforts to restore, monitor, and maintain a functional species–area relationship for future ecosystems. The evolutionary trajectories of the divided population are reflected in the phylogenetic and coalescent histories (*Left*). The networks (*Right*) represent ecological interactions among species in an ecosystem. Monitoring movements, gene flow, or introgression (fusion) of species over fragmented landscapes (fission) is crucial for functional connectivity in conservation practice.

the tone by calling for conservation actions that prioritize evolutionary and ecosystem processes over strict attention to individual species. Noting that most conservation funding has historically been focused on saving the rarest or most charismatic species, with only mixed success, Tobias et al. draw our attention to the processes at the heart of ecosystem function. The authors assert that the three elements of organismal adaptation, movement, and interaction are the cornerstones for effective and sustainable conservation planning, policy, and practice. Among the many points relevant to the focus of this Special Feature, Tobias et al. note that gene flow and organismal dispersal are fundamental for designing and managing landscapes that will enhance species interactions and thus ensure a legacy of resilient ecosystems. The authors make the salient point that animal movement has effects that fundamentally cascade through all relevant trophic levels given (for example) that plants rely heavily on animal dispersal as “mobile links” for seed dispersal. Fundamentally, Tobias et al. call for conservation strategies that focus on preserving and enhancing dispersal and other fundamental processes that connect organisms to their environment.

Increasingly known as the field of “movement ecology,” the study of organismal movement through space and time is fundamental for determining the distribution of genes, individuals, and species (155, 156). Humans have altered the ability of organisms to disperse by altering the landscape via climate change, urbanization, and biological invasions (52), and landscape connectivity is at least in part a function of how and why organisms disperse (157). Managing the dispersal of organisms is included in the 2,030 targets of the Kunming-Montreal Global Biodiversity Framework as part of

the goal of maintaining genetic diversity across all of biodiversity (158), an insight that is drawing increased attention from the conservation community (18).

The paper by Ellis-Soto et al. (30) therefore offers a welcome perspective on how rapidly advancing technologies are providing unprecedented insights into the intricacies of animal movement. The authors describe both the technical and conceptual aspects of “bio-logging” as a means for characterizing bottom-up information on the forces that shape population size and persistence across fragmented landscapes via animal movements. Technological advances are such that multisensor devices can collect real-time data on individual movements and orientation, proximity to other individuals, physiological and stress response, births and deaths, and the relationship of these individual metrics to the landscape. This yields information across multiple scales from individual dispersal patterns to species-level distributions. And in answer to the mandate for ecosystem resilience, analysis of these parameters confers predictive power that can ultimately be employed for conservation design and management. In the authors’ words, technological advances have transformed bio-loggers “from magnifying glasses into microscopes for observing natural processes” while also democratizing biodiversity information in the developing and biodiverse regions of the Earth.

Naidoo et al. (32) conclude the Special Feature with an empirical analysis of the potential for connectivity conservation on large geographic scales. Drawing from detailed experience with conservation projects around the world, the authors describe the successes and failures in four conservation landscapes that represent a diversity of ecosystems and socioeconomic contexts. They find alarmingly that in

three of the landscapes, functional connectivity has declined even after conservation interventions. In developing a “Theory of Change,” Naidoo et al. reinforce the points raised by both Tobias et al. and Ellis-Soto et al. by emphasizing the need to derive connectivity metrics from the study of animal movements, and further, to go beyond a single-species focus by directing action toward multispecies or community-level assessments. Ultimately, they make the point that for conservation strategies to be both practical and sustainable, they must focus on landscape connectivity that has relevance to human socioeconomic and cultural constraints.

In conclusion, the papers in this Special Feature have synergized a process-oriented conservation direction for restoring biodiversity and functional ecosystems in our anthropogenically altered world (Fig. 4). Recent and accruing evidence suggests that gene flow at different temporal and spatial scales has supplied genetic variation for divergent adaptation and the persistence of speciation rates (65, 83, 159–161) against a background of geographic isolation that

mirrors the earliest stages of speciation (73, 162). Therefore, by manipulating the tension between fusion and fission over fragmented habitats, we can effectively conserve both the function and diversity of ecosystems. The speciation literature and its inherent insights can thus inform a conservation sensibility that establishes a spatial, continuous, dynamic foundation for understanding the mechanisms of gene flow and its critical importance for assuring the persistence of Earth’s threatened biodiversity. This perspective urgently awaits integration with conservation science for advancing the possibility, predictability, and performance of conservation practice.

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1. N. M. Haddad et al., Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Sci. Adv.* **1**, e1500052 (2015).
2. J. M. Pandolfi et al., Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**, 955–958 (2003).
3. K. E. Carpenter et al., One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* **321**, 560–563 (2008).
4. G. De’ath, K. E. Fabricius, H. Sweatman, M. Puotinen, The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 17995–17999 (2012).
5. A. M. Dixon, P. M. Forster, S. F. Heron, A. M. K. Stoner, M. Beger, Future loss of local-scale thermal refugia in coral reef ecosystems. *PLoS Climate* **1**, e0000004 (2022).
6. G. N. Daskalova et al., Landscape-scale forest loss as a catalyst of population and biodiversity change. *Science* **368**, 1341–1347 (2020).
7. B. A. Williams et al., Change in terrestrial human footprint drives continued loss of intact ecosystems. *One Earth* **3**, 371–382 (2020).
8. C. Schmidt, M. Domaratzki, R. P. Kinnunen, Continent-wide effects of urbanization on bird and mammal genetic diversity. *Proc. R. Soc. Lond.* **287**, 20192497 (2020).
9. Y. Malhi, T. A. Gardner, G. R. Goldsmith, M. R. Silman, P. Zelazowski, Tropical Forests in the Anthropocene. *Ann. Rev. Environ. Resour.* **39**, 125–159 (2014).
10. T. W. Sherry, Sensitivity of tropical insectivorous birds to the anthropocene: A review of multiple mechanisms and conservation implications. *Front. Ecol. Evol.* **9**, 662873 (2021).
11. E. Elhacham, L. Ben-Uri, J. Grozovski, Y. M. Bar-On, R. Milo, Global human-made mass exceeds all living biomass. *Nature* **588**, 442–444 (2020).
12. C. Rosenzweig et al., Attributing physical and biological impacts to anthropogenic climate change. *Nature* **453**, 353–357 (2008).
13. F. Keck et al., The global human impact on biodiversity. *Nature* **641**, 395–400 (2025).
14. J. R. Allan et al., The minimum land area requiring conservation attention to safeguard biodiversity. *Science* **376**, 1094–1101 (2022).
15. S. Saura et al., Global trends in protected area connectivity from 2010 to 2018. *Biol. Conserv.* **238**, 108183 (2019).
16. M. Ward et al., Just ten percent of the global terrestrial protected area network is structurally connected via intact land. *Nat. Commun.* **11**, 4563 (2020).
17. A. Brennan et al., Functional connectivity of the world’s protected areas. *Science* **376**, 1101–1104 (2022).
18. J. F. Brodie et al., A well-connected earth: The science and conservation of organismal movement. *Science* **388**, eadn2225 (2025).
19. D. R. Williams, C. Rondinini, D. Tilman, Global protected areas seem insufficient to safeguard half of the world’s mammals from human-induced extinction. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2200118119 (2022).
20. W. N. Adger, S. Fransen, R. S. de Campos, W. C. Clark, Scientific frontiers on migration and sustainability. *Proc. Natl. Acad. Sci. U.S.A.* **121**, e2321325121 (2024).
21. S. M. Fitzpatrick, C. M. Giovias, Tropical islands of the anthropocene: Deep histories of anthropogenic terrestrial-marine entanglement in the Pacific and Caribbean. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e202209118 (2021).
22. J. Franklin, G. M. MacDonald, Climate change and California sustainability-Challenges and solutions. *Proc. Natl. Acad. Sci. U.S.A.* **121**, e2405458121 (2024).
23. H. A. Lewin et al., The earth biogenome project 2020: Starting the clock. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2115635118 (2022).
24. S. R. McCouch, L. H. Rieseberg, Harnessing crop diversity. *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2221410120 (2023).
25. J. L. McGuire, A. M. Lawing, S. Diaz, N. C. Stenseth, The past as a lens for biodiversity conservation on a dynamically changing planet. *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2201950120 (2023).
26. N. E. Selin, A. Giang, W. C. Clark, Showcasing advances and building community in modeling for sustainability. *Proc. Natl. Acad. Sci. U.S.A.* **121**, e2215689121 (2024).
27. D. L. Wagner, E. M. Grames, M. L. Forister, M. R. Berenbaum, D. Stopak, Insect decline in the anthropocene: Death by a thousand cuts. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2023989118 (2021).
28. E. S. M. Heijden et al., Genomics of Neotropical biodiversity indicators: Two butterfly radiations with rampant chromosomal rearrangements and hybridization. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410939122 (2025).
29. J. A. Tobias, J. M. Bullock, L. V. Dicks, B. Forester, O. Razgour, Biodiversity conservation requires integration of species-centric and process-based strategies. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410936122 (2025).
30. D. Ellis-Soto et al., From biologging to conservation: Tracking individual performance in changing environments. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410947122 (2025).
31. T. Zhu, Z. Wang, Z. Yang, The power of coalescent methods for inferring recent and ancient gene flow in endangered Bactrian camels. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410949122 (2025).
32. R. Naidoo et al., From science to impact: Conserving ecological connectivity in large conservation landscapes. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410937122 (2025).
33. G. L. Owens et al., A trans-species cytoplasmic polymorphism is associated with seed shape and aridity across multiple species of sunflowers. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410943122 (2025).
34. R. Massatti et al., Suturing fragmented landscapes: Mosaic hybrid zones in plants may facilitate ecosystem resiliency. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410941122 (2025).
35. D. Aguilar-Gómez et al., Genetic rescue of Florida panthers reduced homozygosity but did not swamp ancestral genotypes. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410945122 (2025).
36. A. L. Lewanski et al., Translocations contribute to population rescue in an imperiled woodpecker. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410946122 (2025).
37. G. M. Sgarlata et al., The effect of habitat loss and fragmentation on isolation-by-distance-and-divergence. *bioRxiv* [Preprint] (2024), <https://doi.org/10.1101/2022.10.26.513874> (Accessed 9 May 2025).
38. S. Kong, C. Solis-Lemus, G. P. Tiley, Phylogenetic networks empower biodiversity research. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2410934122 (2025).
39. P. J. Crutzen, Geology of mankind. *Nature* **415**, 23 (2002).
40. S. L. Lewis, M. A. Maslin, Are we in the Anthropocene yet? *Nature* **627**, 466 (2024).
41. J. Zalasiewicz, J. A. Thomas, C. N. Waters, S. Turner, M. J. Head, What should the Anthropocene mean? *Nature* **632**, 980–984 (2024).
42. P. C. M. Crutzen, D. A. Roff, Inbreeding depression in the wild. *Heredity* **83**, 260–270 (1999).
43. B. Hansson, L. Westerberg, On the correlation between heterozygosity and fitness in natural populations. *Mol. Ecol.* **11**, 2467–2474 (2002).
44. D. H. Reed, R. Frankham, Correlation between fitness and genetic diversity. *Conserv. Biol.* **17**, 230–237 (2003).
45. R. Frankham, Genetics and extinction. *Biol. Conserv.* **126**, 131–140 (2005).
46. L. F. Keller, D. M. Waller, Inbreeding effects in wild populations. *Trends Ecol. Evol.* **17**, 230–241 (2002).
47. D. Charlesworth, B. Charlesworth, Inbreeding depression and its evolutionary consequences. *Annu. Rev. Ecol. Syst.* **18**, 237–268 (1987).
48. M. E. Gilpin, M. E. Soulé, “Minimum viable populations: Processes of species extinction” in *Conservation Biology: The Science of Scarcity and Diversity*, M. E. Soulé, Ed. (Sinauer, Sunderland, Mass, 1986), pp. 19–34.
49. M. E. Soulé, What is conservation biology? *Bioscience* **35**, 727–734 (1985).
50. R. K. Didham, V. Kapos, R. M. Ewers, Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* **121**, 161–170 (2012).
51. L. Fahrig, Rethinking patch size and isolation effects: The habitat amount hypothesis. *J. Biogeogr.* **40**, 1649–1663 (2013).
52. K. T. Faulkner, P. E. Hulme, J. R. U. Wilson, Harder, Harder, better, faster, stronger? Dispersal in the anthropocene. *Trends Ecol. Evol.* **39**, 1130–1140 (2024), [10.1016/j.tree.2024.08.010](https://doi.org/10.1016/j.tree.2024.08.010).
53. C. Maré, R. M. Huang, R. A. R. Gulderson, R. J. van Aarde, Protecting and connecting landscapes stabilizes populations of the endangered savannah elephant. *Sci. Adv.* **10**, eadk289 (2024).
54. A. R. Liczner et al., Advances and challenges in ecological connectivity science. *Ecol. Evol.* **14**, e70231 (2024).
55. A. S. Jump, J. Penuelas, Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecol. Lett.* **8**, 1010–1020 (2005).

56. W. F. Fagan, E. E. Holmes, Quantifying the extinction vortex. *Ecol. Lett.* **9**, 51–60 (2006).
57. D. Spielman, B. W. Brook, R. Frankham, Most species are not driven to extinction before genetic factors impact them. *Proc. Natl. Acad. Sci.* **101**, 15261–15264 (2004).
58. R. Lande, Genetics and demography in biological conservation. *Science* **241**, 1455–1460 (1988).
59. D. H. Reed, Extinction risk in fragmented habitats. *Anim. Conserv.* **7**, 181–191 (2004).
60. R. Lande, "Extinction risks from anthropogenic, ecological, and genetic factors" in *Genetics and extinction of species*, L. E. Landweber, A. P. Dobson, Eds. (Princeton University Press, Princeton, NJ, 1999), pp. 1–22.
61. O. Seehausen, G. Takimoto, D. Roy, J. Jokela, Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Mol. Ecol.* **17**, 30–44 (2008).
62. M. A. McQuillan, A. M. Rice, Differential effects of climate and species interactions on range limits at a hybrid zone: Potential direct and indirect impacts of climate change. *Ecol. Evol.* **5**, 5120–5137 (2015).
63. S. A. Taylor, E. L. Larson, R. G. Harrison, Hybrid zones: Windows on climate change. *Trends Ecol. Evol.* **30**, 398–406 (2015).
64. S. F. Ryan *et al.*, Climate-mediated hybrid zone movement revealed with genomics, museum collection, and simulation modeling. *Proc. Natl. Acad. Sci. U.S.A.* **115**, E2284–E2291 (2018).
65. S. Wang *et al.*, Signatures of mitonuclear coevolution in a warbler species complex. *Nat. Commun.* **12**, 4279 (2021).
66. P. R. Grant, B. R. Grant, Hybridization increases population variation during adaptive radiation. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 23216–23224 (2019).
67. S. Wang *et al.*, Selection on a small genomic region underpins differentiation in multiple color traits between two warbler species. *Evol. Lett.* **4**, 502–515 (2020), 10.1002/evl3.198.
68. E. R. Hager *et al.*, A chromosomal inversion contributes to divergence in multiple traits between deer mouse ecotypes. *Science* **377**, 399–405 (2022).
69. G. P. Tilley *et al.*, Estimation of species divergence times in presence of cross-species gene flow. *Syst. Biol.* **72**, 820–836 (2023).
70. P. W. Hedrick, Adaptive introgression in animals: Examples and comparison to new mutation and standing variation as sources of adaptive variation. *Mol. Ecol.* **22**, 4606–4618 (2013).
71. A. Suarez-Gonzalez, C. Lexer, Q. C. B. Cronk, Adaptive introgression: A plant perspective. *Biol. Lett.* **14**, 20170688 (2018).
72. A. H. Patton, E. J. Richards, K. J. Gould, L. K. Buie, C. H. Martin, Hybridization alters the shape of the genotypic fitness landscape, increasing access to novel fitness peaks during adaptive radiation. *eLife* **11**, e72905 (2022).
73. E. Mayr, *Systematics and the Origin of Species from the Viewpoint of a Zoologist* (Harvard University Press, Cambridge, MA, 1942).
74. L. Croizat, *Panbiogeography or An Introductory Synthesis of Zoogeography, Phytogeography, Geology; with notes on evolution, systematics, ecology, anthropology* (Caracas, Venezuela, 1958).
75. A. D. Yoder *et al.*, A multidimensional approach for detecting species patterns in Malagasy vertebrates. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 6587–6594 (2005).
76. E. Mayr, *Animal Species and Evolution* (Harvard University Press, Cambridge, MA, 1963), p. 797.
77. R. A. Fisher, *The Genetical Theory of Natural Selection* (The Clarendon Press, 1930).
78. J. A. Coyne, H. A. Orr, *Speciation* (Sinauer Associates, Sunderland, MA, 2004).
79. K. L. Shaw, S. P. Mullen, Speciation continuum. *J. Hered.* **105**, 741–742 (2014).
80. C. Roux *et al.*, Shedding light on the grey zone of speciation along a continuum of genomic divergence. *PLoS Biol.* **14**, e2000234 (2016).
81. S. Stankowski, M. Ravinet, Defining the speciation continuum. *Evolution* **75**, 1256–1273 (2021), 10.1111/evo.14215.
82. P. S. Soltis, D. E. Soltis, The role of hybridization in plant speciation. *Annu. Rev. Plant Biol.* **60**, 561–588 (2009).
83. N. B. Edelman, J. Mallet, Prevalence and adaptive impact of introgression. *Annu. Rev. Genet.* **55**, 265–283 (2021).
84. M. L. Rosenzweig, Loss of speciation rate will impoverish future diversity. *Proc. Natl. Acad. Sci. U.S.A.* **98**, 5404–5410 (2001).
85. J. Felsenstein, Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* **35**, 124–138 (1981).
86. J. L. Feder, S. P. Egan, P. Nosil, The genomics of speciation-with-gene-flow. *Trends Genet.* **28**, 342–350 (2012).
87. M. Kirkpatrick, V. Ravigne, Speciation by natural and sexual selection: Models and experiments. *Am. Nat.* **159**, S22–35 (2002).
88. G. G. Mittelbach *et al.*, Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecol. Lett.* **10**, 315–331 (2007).
89. O. Seehausen *et al.*, Genomics and the origin of species. *Nat. Rev. Genet.* **15**, 176–192 (2014).
90. B. A. Payseur, L. H. Rieseberg, A genomic perspective on hybridization and speciation. *Mol. Ecol.* **25**, 2337–2360 (2016).
91. C. R. Campbell, J. Poelstra, A. D. Yoder, What is speciation genomics? The roles of ecology, gene flow, and genomic architecture in the formation of species. *Biol. J. Linn. Soc.* **124**, 561–583 (2018).
92. R. K. Butlin *et al.*, Homage to Felsenstein 1981, or why are there so few many species? *Evolution* **75**, 978–988 (2021).
93. A. M. Westram, S. Stankowski, P. Surendranadh, N. Barton, What is reproductive isolation? *J. Evol. Biol.* **35**, 1143–1164 (2022).
94. J. A. Endler, *Geographic Variation, Speciation and Clines* (Princeton University Press, 1977), vol. 10.
95. N. H. Barton, The dynamics of hybrid zones. *Heredity* **43**, 341–359 (1979).
96. N. H. Barton, The role of hybridization in evolution. *Mol. Ecol.* **10**, 551–568 (2001).
97. L. H. Rieseberg, Chromosomal rearrangements and speciation. *Trends Ecol. Evol.* **16**, 351–358 (2001).
98. D. Schluter, G. L. Conte, Genetics and ecological speciation. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 9955–9962 (2009).
99. L. H. Rieseberg, B. K. Blackman, Speciation genes in plants. *Ann. Bot.* **106**, 439–455 (2010).
100. B. L. Anacker, S. Y. Strauss, The geography and ecology of plant speciation: Range overlap and niche divergence in sister species. *Proc. Biol. Sci.* **281**, 20132980 (2014).
101. W. L. Brown, Centrifugal speciation. *Q. Rev. Biol.* **32**, 247–277 (1957).
102. R. H. MacArthur, E. O. Wilson, "The theory of island biogeography" in *Princeton Landmarks in Biology* (Princeton University Press, 1967).
103. M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge University Press, ed. 1, 1995).
104. J. B. Losos, D. Schluter, Analysis of an evolutionary species-area relationship. *Nature* **408**, 847–850 (2000).
105. B. R. Grant, P. R. Grant, What Darwin's finches can teach us about the evolutionary origin and regulation of biodiversity. *Bioscience* **53**, 965–975 (2003).
106. X. Y. Chen, F. He, Speciation and endemism under the model of island biogeography. *Ecology* **90**, 39–45 (2009).
107. J. B. Losos, Ecological and evolutionary determinants of the species-area relation in Caribbean anoline lizards. *Philos. Trans. R. Soc. B-Biol. Sci.* **351**, 847–854 (1996).
108. B. C. Emerson, N. Kolm, Species diversity can drive speciation. *Nature* **434**, 1015–1017 (2005).
109. 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).
110. D. Schluter, Experimental-evidence that competition promotes divergence in adaptive radiation. *Science* **266**, 798–801 (1994).
111. A. W. Jones, D. M. Post, Does intraspecific competition promote variation? A test via synthesis. *Ecol. Evol.* **6**, 1646–1655 (2016).
112. A. Estrada *et al.*, Impending extinction crisis of the world's primates: Why primates matter. *Sci. Adv.* **3**, e1600946 (2017).
113. S. A. Cushman, Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biol. Conserv.* **128**, 231–240 (2006).
114. T. Aavik, A. Helm, Restoration of plant species and genetic diversity depends on landscape-scale dispersal. *Restor. Ecol.* **26**, S92–S102 (2017).
115. F. P. Palstra, D. E. Ruzzante, Genetic estimates of contemporary effective population size: What can they tell us about the importance of genetic stochasticity for wild population persistence? *Mol. Ecol.* **17**, 3428–3447 (2008).
116. C. A. Stockwell, A. P. Hendry, M. T. Kinnison, Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* **18**, 94–101 (2003).
117. S. R. Loss, L. A. Terwilliger, A. C. Peterson, Assisted colonization: Integrating conservation strategies in the face of climate change. *Biol. Conserv.* **144**, 92–100 (2011).
118. M. Baguette, H. Van Dyck, Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal. *Landscape Ecol.* **22**, 1117–1129 (2007).
119. M. Pfeifer *et al.*, Creation of forest edges has a global impact on forest vertebrates. *Nature* **551**, 187–191 (2017).
120. B. A. Wintle *et al.*, Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 909–914 (2019).
121. S. Saura, Ö. Bodin, M. J. Fortin, J. Frair, Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *J. Appl. Ecol.* **51**, 171–182 (2013).
122. S. W. Fitzpatrick, C. Mitten-Moreau, M. Miller, J. M. Judson, Genetic rescue remains underused for aiding recovery of federally listed vertebrates in the United States. *J. Hered.* **114**, 354–366 (2023).
123. R. Frankham, Genetic rescue of small inbred populations: Meta-analysis reveals large and consistent benefits of gene flow. *Mol. Ecol.* **24**, 2610–2618 (2015).
124. S. L. Pimm, L. Dollar, O. L. Bass, The genetic rescue of the Florida panther. *Anim. Conserv.* **9**, 115–122 (2006).
125. E. Zhivkopoulos, J. M. Silva, R. Blasiak, How transdisciplinarity can help biotech-driven biodiversity research. *Trends Biotechnol.* (2025), 10.1016/j.tibtech.2025.04.008.
126. A. R. Whiteley, S. W. Fitzpatrick, W. C. Funk, D. A. Tallmon, Genetic rescue to the rescue. *Trends Ecol. Evol.* **30**, 42–49 (2015).
127. D. E. Rosen, Vicariant patterns and historical explanation in biogeography. *Syst. Zool.* **27**, 159–188 (1978).
128. R. J. Stern, The evolution of plate tectonics. *Philos. Trans. R. Soc. Lond. A Math. Phys. Eng. Sci.* **376**, 20170406 (2018).
129. A. L. Rand, Glaciation, an isolating factor in speciation. *Evolution* **2**, 314–321 (1948).
130. A. D. Barnosky, P. L. Koch, R. S. Feranec, S. L. Wing, A. B. Shabel, Assessing the causes of late Pleistocene extinctions on the continents. *Science* **306**, 70–75 (2004).
131. J. T. Weir, D. Schluter, Ice sheets promote speciation in boreal birds. *Proc. Biol. Sci.* **271**, 1881–1887 (2004).
132. I. J. Lovette, Glacial cycles and the tempo of avian speciation. *Trends Ecol. Evol.* **20**, 57–59 (2005).
133. E. Bermingham, S. Rohwer, S. Freeman, C. Wood, Vicariance biogeography in the Pleistocene and speciation in North American wood warblers, a test of Mengel's model. *Proc. Nat. Acad. Sci., U.S.A.* **89**, 6624–6628 (1992).
134. J. C. Avise, D. Walker, Pleistocene phylogeographic effects on avian populations and the speciation process. *Proc. R. Soc. Lond. B* **265**, 457–463 (1998).
135. E. C. Corrick *et al.*, Synchronous timing of abrupt climate changes during the last glacial period. *Science* **369**, 963–969 (2020).
136. D. R. Schlaepfer, B. Braschler, H. Rusterholz, B. Baur, Genetic effects of anthropogenic habitat fragmentation on remnant animal and plant populations: A meta-analysis. *Ecosphere* **9**, e02488 (2018).
137. I. Saccheri *et al.*, Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**, 491–494 (1998).
138. M. J. Hickerson *et al.*, Phylogeography's past, present, and future: 10 years after Avise, 2000. *Mol. Phylogenet. Evol.* **54**, 291–301 (2010).
139. L. Naughton-Treves, M. B. Holland, K. Brandon, The role of protected areas in conserving biodiversity and sustaining local livelihoods. *Annu. Rev. Environ. Resour.* **30**, 219–252 (2005).

140. V. Vijay, P. R. Armsworth, Pervasive cropland in protected areas highlight trade-offs between conservation and food security. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2010121118 (2021).
141. J. Geldmann, A. Manica, N. D. Burgess, L. Coad, A. Balmford, A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 23209–23215 (2019).
142. G. Li *et al.*, Global impacts of future urban expansion on terrestrial vertebrate diversity. *Nat. Commun.* **13**, 1628 (2022).
143. R. M. Pringle, Upgrading protected areas to conserve wild biodiversity. *Nature* **546**, 91–99 (2017).
144. C. Kremen, A. M. Merenlender, Landscapes that work for biodiversity and people. *Science* **362**, eaau6020 (2018).
145. D. Tilman *et al.*, Future threats to biodiversity and pathways to their prevention. *Nature* **546**, 73–81 (2017).
146. V. Arroyo-Rodriguez *et al.*, Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecol. Lett.* **23**, 1404–1420 (2020).
147. G. Keppel, D. Stralberg, T. L. Morelli, Z. Batori, Managing climate-change refugia to prevent extinctions. *Trends Ecol. Evol.* **39**, 800–808 (2024).
148. S. Gomez *et al.*, Understanding and predicting animal movements and distributions in the anthropocene. *J. Anim. Ecol.* **94**, 1146–1164 (2025), 10.1111/1365-2656.70040.
149. M. E. Maan, O. Seehausen, Ecology, sexual selection and speciation. *Ecol. Lett.* **14**, 591–602 (2011).
150. S. P. Turbek, E. S. C. Scordato, R. J. Safran, The role of seasonal migration in population divergence and reproductive isolation. *Trends Ecol. Evol.* **33**, 164–175 (2018).
151. D. R. de Zwaan, J. Mackenzie, E. Mikkelsen, C. Wood, S. Wang, Pleiotropic opposing dominance within a color gene block contributes to a nascent species boundary via its influence on hybrid male territorial behavior. *PNAS Nexus* **1**, pgac074 (2022).
152. M. I. M. Louder *et al.*, Gene regulation and speciation in a migratory divide between songbirds. *Nat. Commun.* **15**, 98 (2024).
153. T. H. Oliver *et al.*, Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* **30**, 673–684 (2015).
154. T. Goncalves-Souza *et al.*, Species turnover does not rescue biodiversity in fragmented landscapes. *Nature* **640**, 702–706 (2025), 10.1038/s41586-025-08688-7.
155. F. Jeltsch *et al.*, Integrating movement ecology with biodiversity research - Exploring new avenues to address spatiotemporal biodiversity dynamics. *Mov. Ecol.* **1**, 6 (2013).
156. T. S. Doherty, D. A. Driscoll, Coupling movement and landscape ecology for animal conservation in production landscapes. *Proc. Biol. Sci.* **285**, 20172272 (2018).
157. M. Baguette, S. Blanchet, D. Legrand, V. M. Stevens, C. Turlure, Individual dispersal, landscape connectivity and ecological networks. *Biol. Rev. Camb. Philos. Soc.* **88**, 310–326 (2013).
158. A. Mastretta-Yanes *et al.*, Multinational evaluation of genetic diversity indicators for the Kunming-Montreal Global Biodiversity Framework. *Ecol. Lett.* **27**, e14461 (2024).
159. J. Y. Choi *et al.*, Ancestral polymorphisms shape the adaptive radiation of *Metrosideros* across the Hawaiian Islands. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2023801118 (2021).
160. J. I. Meier *et al.*, Cycles of fusion and fission enabled rapid parallel adaptive radiations in African cichlids. *Science* **381**, 1428 (2023).
161. L. M. Blumer *et al.*, Introgression dynamics of sex-linked chromosomal inversions shape the Malawi cichlid adaptive radiation. *bioRxiv* [Preprint] (2025), 10.1101/2024.07.28.605452.
162. T. Dobzhansky, *Genetics and the Origin of Species* (Columbia University Press, New York, 1937).