Rebuilding Diversity in the Anthropocene

Authors: Christian Voolstra[1]*, Ruben J. Hermann[1], Herwig Stibor[2], Alexander Keller[2], Lutz Becks[1]*

* Corresponding authors: christian.voolstra@uni-konstanz.de, lutz.becks@uni-konstanz.de

[1] Department of Biology, University of Konstanz, 78464 Konstanz, Germany

[2] Faculty of Biology, Ludwig-Maximilians-Universität München, 82152 Planegg-Martinsried, Germany

Abstract

Rapid changes driven by the Anthropocene—including shifts in climate, nutrients, habitats, and species composition—are causing severe biodiversity loss while creating new ecological opportunities. The balance between short-term ecological shifts in realized niches and long-term evolutionary changes in fundamental niches determines diversification. In the Anthropocene, however, this balance is unstable, as environmental turnover often outpaces adaptive evolution. Processes such as interaction-network rewiring, mutualism loss or emergence, and microbiome-mediated plasticity can hinder or promote diversification. Identifying when opportunities persist, drive fundamental niche evolution, and enable biodiversity to withstand or recover from rapid global change requires a predictive framework linking ecological dynamics, evolutionary mechanisms, and host–microbiome interactions.

Main

Biodiversity is a dynamic and vital component of ecosystems, playing a critical role in ecological processes, the overall functioning of the environment, and the provisioning of ecosystem services. A key concept in understanding changes in biodiversity is ecological opportunity [1,2]. In Hutchinsonian niche terms, ecological opportunity arises when unoccupied or underutilized portions of niche space become available. These opportunities can be taken up by individuals with suitable traits, leading in the short term to shifts or expansions of their realized niche, the actual subset of conditions and resources used in nature under ecological constraints. When ecological opportunity persists and diversifying selection acts on heritable variation, these ecological responses may, over evolutionary time, alter the fundamental niche itself by expanding physiological tolerances or generating new adaptations [3,4]. In this way, ecological opportunity links ecological adjustments to long-term evolutionary diversification. Ecological opportunity has long been used to explain diversification and predict diversity equilibria in scenarios such as the colonisation of new environments or new islands, habitat shifts, the evolution of key innovations, or the extinction of antagonistic species [5]. In such cases, unoccupied niches allowed realized niches to expand, and sustained diversifying selection subsequently produced adaptive radiations and long-term increases in diversity. However, the relationship between ecological opportunity and diversification in the context of ongoing anthropogenic change is less well understood.

In the present era, rapid biodiversity loss coincides with equally rapid abiotic change. In theory, this combination should create abundant ecological opportunity and drive diversification. Yet, we argue that the conditions of the Anthropocene are markedly

different from past eras, and, more importantly, that the current framework for understanding ecological opportunity is inadequate to fully capture or predict changes in extant biodiversity. While current biodiversity declines mirror past events in which major physical perturbations triggered mass extinctions, followed by periods of high diversification driven by newly available ecological opportunities [6,7], the rapid pace and scale of contemporary environmental change present unique challenges. The speed at which these changes occur may destabilize existing ecological niches before evolutionary processes have a chance to respond. This paper explores the limitations of the existing framework and proposes a novel assessment of how we understand ecological opportunity in the context of the Anthropocene. This extended conceptual framework provides a path to start determining the conditions under which biodiversity can rebuild in this era.

Ecological opportunity and diversification in brief

For ecological opportunity to generate diversification, four key conditions must be met. These conditions operate across two levels: ecological time, where populations adjust their realized niches, and evolutionary time, where selection and adaptation reshape the fundamental niche. If any one of these conditions is not met, diversification will not occur.

Condition 1. **Niche availability** (ecological): There must be unoccupied or underutilized niche space that populations can exploit. In ecological time, this may result in rapid shifts or expansions of the realized niche, sometimes through behavioral flexibility,

65 migration or ecological plasticity alone. If niche space can be fully occupied in this way,
66 further diversification is not required.

67 Condition 2. **Niche discordance and diversifying selection** (ecological to
68 evolutionary): When available niche space is not fully filled by realized niche shifts, a
69 mismatch remains between environmental conditions and population traits. This niche
70 discordance creates ecological opportunity that, if heritable variation exists, exposes
71 populations to diversifying selection. Over time, this process drives adaptive divergence
72 and sets the stage for evolutionary change in the fundamental niche.

73 Condition 3. **Selection consistency** (evolutionary): For diversification to occur, the
74 form, direction, and intensity of selection must remain consistent across time and/or
75 space. If environmental conditions fluctuate too quickly, or competitors occupy the
76 niche, selection pressures dissipate and diversification fails.

77 Condition 4. **Diversification potential** (evolutionary): Successful evolutionary
78 diversification requires genetic and phenotypic variation sufficient for populations to
79 respond to selection. Without this, realized niche adjustments remain transient and
80 cannot be translated into long-term shifts in the fundamental niche.

81 Past examples, such as island colonization or the evolution of key innovations,
82 show how ecological opportunity can move from realized niche adjustments to
83 fundamental niche evolution. While we have some understanding of how these four key
84 conditions contribute to diversification, much remains unknown about how they interact
85 across different temporal and spatial scales, particularly in the Anthropocene and the
86 ongoing biodiversity loss. Under anthropogenic change, niche opportunities may arise

but vanish too quickly or be destabilized before selection can act, leaving realized niche shifts without evolutionary follow-through. This temporal mismatch threatens the capacity of biodiversity to regenerate in the Anthropocene. Yet understanding how anthropogenic change and ongoing biodiversity loss influence niche availability, niche discordance, consistency of selection, and the potential for diversification is essential for predicting the future of biodiversity. This knowledge is increasingly important as we face accelerating rates of species extinction and ecosystem degradation, and is crucial for developing effective conservation strategies to preserve the processes that drive evolutionary change. It also provides a framework to restore or produce conditions conducive to increasing diversity.

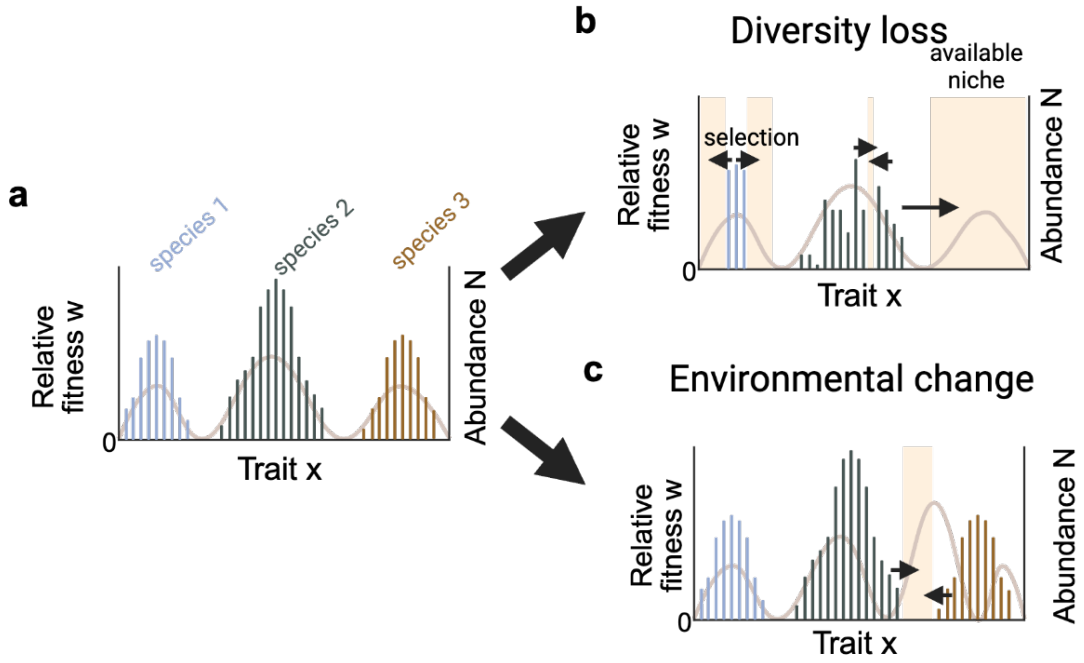

Figure 1: Diversity and the impact of anthropogenic change. *a) An illustration depicting fitness and abundance in a hypothetical three-species community, with individuals (vertical bars) exhibiting trait variation both within and between species. Abundances of individuals with a trait value x reflect their fitness distribution, shaped by prior selection. b,c) Scenarios of anthropogenic change that trigger biotic and/or abiotic changes, leading to ecological opportunity. b) Biodiversity loss is characterized by individuals and trait diversity being lost from the community, e.g. through extreme weather events. c) Similarly, environmental changes, e.g. through habitat fragmentation, salinification, or local climate changes, are characterized by fitness landscape shifts due to altered abiotic conditions or species interactions. These changes can create opportunities in the form of unoccupied niches and niche discordance, resulting in new selection pressures (indicated by arrows) that can be exploited and drive the rebuilding of biodiversity).*

The Anthropocene changes the game field

Although the start of the Anthropocene is debated, what is indisputable is the profound and unprecedented impact humans have had on the environment [8,9]. Rapid and continuous growth in human activities, including the overuse of resources, habitat destruction, and the burning of fossil fuels, has driven substantial and rapid environmental changes, such as rising global temperatures and increasing frequency of extreme weather events [8,10]. These changes are reshaping biodiversity, causing the loss of species, phenotypic variation, and genetic diversity [11], while homogenizing biological communities across regions and communities (e.g, microbes, plants and mobile animals). The Anthropocene is hence characterized by an accelerating loss of biodiversity, sometimes referred to as the sixth mass extinction [12–14], in addition to the multiple rapid environmental changes that signify the current era (Table 1).

For consideration of the conditions under which biodiversity is rebuilt, the Anthropocene profoundly alters the four key conditions that shape ecological opportunity and diversification: niche availability, niche discordance, selection consistency, and diversification potential. In Hutchinsonian terms, these changes affect both realized niche space (short-term ecological adjustments) and fundamental niche space (long-term evolutionary potential). In this era, niches often open up more quickly and frequently due to rapid environmental changes, such as habitat loss, climate change, or the introduction of invasive species. These shifts can create novel ecological opportunities by releasing species from antagonistic interactions, such as competition and predation [15]. This allows certain species to expand their population size and habitat use rapidly [16,17]. However, these opportunities are often short-lived, as niches may close

just as quickly if environmental conditions continue to change faster than organisms can adapt. By contrast, under the more stable conditions of the pre-Anthropocene era, niche availability tended to be less dynamic and more persistent.

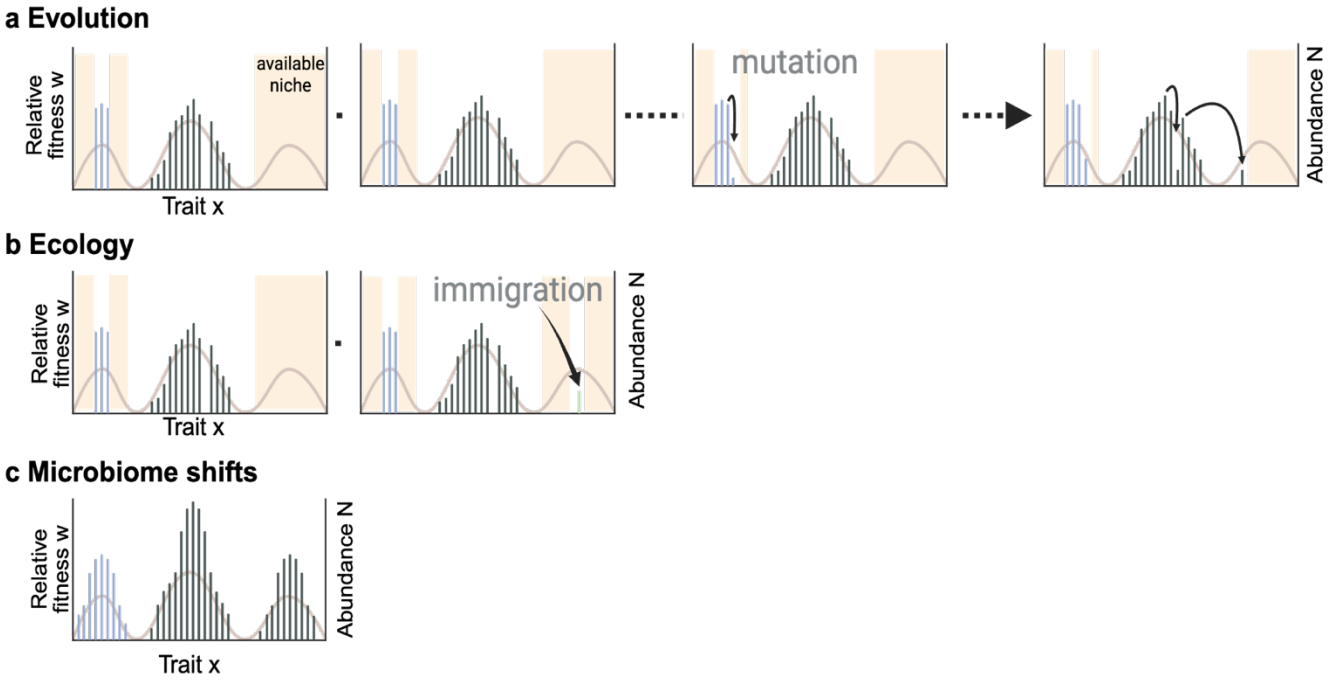

Figure 2: Pathways of diversity buildup. *The initial biodiversity loss (see also Fig. 1b) as a consequence of anthropogenic change can provide opportunities, i.e. available niches (e.g. resources in the form of nutrients, energy, space, information) that become accessible and can drive recovery of biodiversity. Different mechanisms enable the filling of available niches and support the build-up of diversity over time. Dashed lines indicate the numbers of generations, from a few to 1000s. a) Evolution: Despite strong selection, available niches remain unoccupied for several generations. Only gradually do mutations arise, mutations occurring with a higher probability when abundance is high. b) Ecology: immigration from other populations or dormant stages can introduce species that occupy new and available niches. c) Microbiome shifts: Rapid changes in the microbiome associated with individuals of certain trait values can facilitate quick niche occupation.*

Niche discordance—the mismatch between an individual's ecological requirements and its environment—is a fundamental driver of evolutionary change, and the rapid, unpredictable environmental shifts characteristic of the Anthropocene frequently exacerbate these mismatches. For instance, invasive species can alter resource availability, forcing native species to adapt to new niches or face increased competition [18]. Meanwhile, rapid abiotic changes can shift optimal trait values, thereby exacerbating niche discordance. These mismatches create temporary ecological opportunities, but unless they stabilize, they lead only to transient realized niche adjustments rather than sustained fundamental niche evolution. While such discordance can intensify diversifying selection, the overall effect is complex. Declining population densities, a hallmark of the Anthropocene [19–21], can reduce the intensity of competition and thus diminish the opportunities for niche discordance to drive diversification.

For selection to result in long-term diversification, environmental pressures must be consistent over time and across space. However, the Anthropocene is characterized by highly unpredictable, frequent, and abrupt environmental changes, such as those driven by ongoing climate change or habitat fragmentation, which undermine the consistency of selection and reduce the likelihood of new adaptations persisting long enough to lead to expand the fundamental niche and finally to diversification (Fig. 1). While some niches, such as those found in urban environments, may remain stable enough for adaptation and diversification to occur [22], many others are too transient for evolutionary processes to take hold.

The potential for diversification is further constrained by the loss of genetic diversity resulting from habitat destruction and fragmentation, as well as other human

172 impacts. Reduced genetic diversity limits the raw material for evolution; with fewer
173 alleles in the population, the likelihood of novel genetic combinations arising through
174 recombination decreases. Small population sizes reduce the supply of new mutations
175 and increase the effects of genetic drift. Conversely, larger populations in more stable
176 environments typically harbor greater genetic diversity and a richer supply of mutations,
177 thereby enhancing diversification potential [23]. Thus, even when realized niches expand
178 ecologically, the erosion of diversification potential prevents these expansions from
179 being consolidated into new fundamental niches.

180 Interestingly, strong directional selection resulting from rapid environmental
181 change can reduce both interspecific and intraspecific trait variation. For example,
182 habitat fragmentation and homogenization as well as land-use intensification favors
183 generalists over specialists [24,25], while temperature increases reduce intraspecific
184 variation in fish [26]. Here, realized niches converge under ecological time, but narrowing
185 variation reduces the scope for diversifying selection to open new evolutionary
186 pathways. However, some studies have shown that different mutations and genotypes
187 can exhibit increased fitness under these conditions [27,28], which could promote trait
188 diversification and set the stage for adaptive radiation.

189 Anthropogenic changes also reshape species interactions in multiple ways, often
190 reducing mutualistic relationships. This erosion of mutualisms can lead to delayed
191 secondary extinctions through extinction debts [29]. Alongside such losses, however,
192 facilitation debts may also occur, i.e. the delayed appearance of positive interactions
193 when species establish mutualisms previously absent in a system, potentially creating
194 new ecological opportunities for diversification. Moreover, rewired communities can

generate novel mutualistic interactions, for example between native and non-native species, which may temporarily expand realized niche space and open new pathways for diversification. At the same time, mutualisms may shift toward antagonistic interactions [30–32]. Antagonistic interactions, such as predator–prey and host–parasite dynamics, are well-known drivers of diversification, though the long-term consequences of widespread mutualism breakdown remain uncertain. Invasive species, heavily facilitated by globalization and other anthropogenic drivers, often have further impacts on local communities for example through their effects on the rewiring of the communities and the dominance of domesticated species (e.g., honey bees competing with wild bees; [33,34]).

In summary, the Anthropocene accelerates the opening and closing of realized ecological niches (ecological time), destabilizes the conditions needed for realized shifts to accumulate into fundamental niche change (evolutionary time), increases niche discordance through rapid environmental change, undermines the consistency of selection, and erodes the genetic diversity necessary for long-term diversification. While these pressures threaten and decimate existing biodiversity, they also reshape the evolutionary landscape, with the possibility of sometimes creating novel opportunities for diversification even as they close others (Fig. 2).

Table 1: Hallmarks and characteristics of the Anthropocene condition

Anthropocene conditions	Non-Anthropocene conditions	Example for Anthropocene condition	Expected effect for key conditions of ecological opportunity in the Anthropocene

Rapid loss of biodiversity	'Turn over' of biodiversity (on average over time and space)	Extinctions and biomass decline [12,20] Loss of genetic diversity [23] Homogenization of communities [35]	niche availability: fluctuating niche discordance: higher (stronger mismatch between traits and environment), or lower when competition is lower selection consistency: lower diversification potential: lower
Abiotic change rapid, continuous	Abiotic change slow (on average)	Climate change [36] Fragmentation [37,38] Weather extremes [37–39]	niche availability: fluctuating niche discordance: higher selection consistency: lower diversification potential: lower
Biomass highly dynamic, not at equilibrium often declining	Biomass closer to equilibrium	Shifting biomass [16,40] Biomass decline in insects [20,21]	niche availability: fluctuating niche discordance: higher, or lower when competition is lower selection consistency: lower diversification potential: lower (e.g., through the effect of drift)
Traits that determine species interactions change rapidly	Only some traits that determine species interactions change rapidly	Switch from mutualism to antagonism [30,31] Plant-pollinator mismatch [41,42])	niche availability: fluctuating niche discordance: higher, or lower when competition is lower selection consistency: lower diversification potential: lower (e.g., through the effect of drift)
Intra- and	Intra- and	Competitive	niche availability: lower

interspecific trait (co)variation limited due to "extreme" selection	interspecific trait (co)variation variable/high	exclusion of specialists [24] Reduction intraspecific variation (Morgan et al, 2020; [43]	niche discordance: lower (diversifying selection is low) selection consistency: higher diversification potential: lower (e.g., through the effect of drift)

Beyond evolution

The key challenge in understanding biodiversity changes in the Anthropocene lies in determining when the conditions for ecological opportunity and diversification align with the rate of environmental change and ongoing biodiversity loss. Since ecological opportunity and diversification rely on all key conditions being met, we would generally expect the potential for diversification under Anthropocene conditions to be low, as at least one of these conditions is likely to be negatively affected, leading to further biodiversity decline (Table 1). However, by integrating ecological dynamics (i.e., patterns and processes of change in ecological systems over time and space, e.g. population/community dynamics, disturbance and succession, etc.) and considering the role of the microbiome in supporting host environmental adaptation (e.g., by altering metabolic capacity or stress tolerance through association with novel microbes) [44] within the framework of ecological opportunity and diversification, the outlook becomes less dire, revealing a greater potential for generating and rebuilding diversity despite the ongoing challenges.

Incorporating ecological context and microbiome dynamics extends our understanding of ecological opportunity by adding complexity, plasticity, and temporal variability to its core components. As **niche availability** is not solely determined by

232 evolutionary change, alternative mechanisms rooted in ecological dynamics and
233 microbiome shifts must also be considered. Ecological processes such as migration,
234 changes in population size, or community turnover can reshape which niches are
235 occupied or accessible, without necessitating genetic change in the populations
236 involved. For example, migration enables species to track favorable conditions or avoid
237 competition, thereby opening or closing niches as populations move in response to
238 environmental variability or disturbance [45–47]. Similarly, fluctuations in population size
239 driven by birth and death rates, dispersal, or local extinctions can make previously
240 occupied niches available to other species or lead to niche saturation when populations
241 grow or aggregate [48]. Community-level processes such as colonisation and species
242 turnover also contribute to these dynamics, as the arrival or loss of species can instantly
243 alter the competitive landscape and resource availability (between-organismal
244 interactions; Fig. 2b). These ecological processes operate on realized niche space,
245 altering which parts of the hypervolume are currently occupied, without requiring
246 changes to the fundamental niche.
247 When microbiome-mediated adaptation is included within-host organismal
248 interactions change, and niche availability may in fact decrease, as rapid microbial
249 turnover can allow host organisms to rapidly exploit emerging niches, potentially
250 saturating them before other mechanisms of adaptation can act (Fig. 2c). In
251 Hutchinsonian terms, microbiomes can both constrain and expand host niche space: on
252 the one hand, they can quickly saturate emerging niches; on the other, they can
253 establish novel mutualistic associations that extend the realized niche into holobiont
254 conditions otherwise outside its host physiological tolerance. Such expansions can

create rapid ecological responses and, if persistent, provide stepping stones toward fundamental niche evolution. However, reliance on microbial plasticity may also reduce host long-term diversification if it consistently substitutes for genetic adaptation. Together, these additional mechanisms of ecological shifts and microbiome dynamics demonstrate that niche availability is a highly variable and largely unaccounted property of ecosystems. Importantly, these mechanisms are poised to create, modify, or eliminate ecological opportunities far more rapidly than ecological changes or evolutionary adaptation can occur, which highlights the importance of considering both ecological and evolutionary perspectives (and the inherent timescales) when assessing the drivers of biodiversity and community structure.

Second, **niche discordance** can become more pronounced through ecological mechanisms. Rapid changes in community composition, migration, or population density can swiftly alter the local environment, resulting in mismatches between individuals' traits and the conditions they encounter. The arrival of new competitors, predators or mutualists, or the sudden loss of key species, for example, can disrupt established ecological relationships and create new axes of trait–environment discordance [49,50]. These ecological shifts may promote diversifying selection, forcing organisms to adapt to novel or fluctuating conditions. Alternatively, they may increase the risk of maladaptation if changes occur too quickly for populations to respond [28,51]. Microbiome dynamics might further amplify this effect. For instance, the arrival or loss of specific microbial taxa or genotypes can shift host phenotypes in ways that increase or buffer discordance, introducing novel axes of trait–environment mismatches and promoting diversifying selection or maladaptation, thus shaping whether realized niche

shifts translate into evolutionary pathways toward new fundamental niches [52]. Together, ecological mechanisms and microbiome shifts emphasize the complexity and dynamism of niche discordance, demonstrating how both can influence evolutionary responses in changing environments.

Third, **selection consistency** is reduced when ecological factors such as species turnover and community shifts cause niches to open or close dynamically. This makes ecological opportunity a moving target. Microbiome-driven phenotypic plasticity enables hosts to access transient niches through microbial shifts, stabilizing short-term niche occupation but diminishing the cumulative selection pressures required for long-term niche evolution.

Finally, the **diversification potential** depends on the generation and maintenance of trait variation. While traditional evolutionary mechanisms such as mutation, genetic recombination, or hybridization are important sources of this variation, ecological mechanisms and microbiome shifts can play a crucial role. Processes such as migration and changes in population size can rapidly introduce new genetic and phenotypic variants into populations or alter the relative abundance of existing ones [47,53,54]. This increases or decreases the pool of available diversity. It is important to note that niches are not only filled by new variants arising within a population, but also by new species moving in from elsewhere. The immigration of new species can quickly occupy open niches, sometimes outcompeting resident populations or preventing local diversification by monopolizing resources [55–57]. Consequently, diversity within species (intraspecific variation) and diversity between species (interspecific variation) may compete with each other, influencing which lineages are able to establish, persist, and

diversify in a given ecological context. Mutualistic networks can also enhance diversification potential by sustaining larger and more genetically diverse populations, thereby maintaining the raw material for evolutionary change. For instance, plant–pollinator or seed-dispersal interactions can buffer small populations from collapse, prolonging their persistence until diversification becomes possible. Microbiome shifts add another layer of complexity to this dynamic: by modifying host phenotypes, they change realized niche occupation and sometimes open temporary access to new resources, but they can also close pathways toward fundamental niche evolution by short-circuiting selection [58–60]. Microbial communities are shaped by intense competition and cooperation, which often leads to niche differentiation or exclusion within the microbiome. When they restructure, microbiomes can facilitate or constrain diversification by modifying the ecological opportunities available to their hosts and accessible by their hosts, thereby influencing which microbial and host lineages thrive or decline. Therefore, the interplay between genetic, ecological, and microbiome-mediated mechanisms determines how niches are filled and how diversity builds up.

Conclusion

Understanding how biodiversity can persist or rebuild under Anthropocene conditions requires rethinking and extending classical evolutionary concepts of diversification and ecological opportunity by integrating ecological adjustments in realized niche space and evolutionary change in fundamental niche space. The Anthropocene is characterized by unprecedented rates of abiotic change, biodiversity loss, and ecological disruption, which simultaneously open and close niches in unpredictable ways. Unlike recovery

processes such as ecological succession or post-disturbance assembly, Anthropocene conditions lack a stable baseline and often undermine the very mechanisms—trait variation, consistent selection, and ecological coherence—required for diversification to occur. In this context, the potential to rebuild diversity depends on identifying when and how the key conditions for ecological opportunity align with the velocity of environmental change.

Bridging evolutionary biology to ecology and incorporating microbiota-mediated responses is essential to unify classical theories of diversification and ecological opportunity with the successional dynamics of communities and species interactions. Ecological processes such as species movement, community turnover, and altered interactions reshape niche availability, discordance, and selection regimes, making ecological opportunity a temporally dynamic and spatially contingent phenomenon. Adaptation by means of host-associated microbiome changes further adds complexity, enabling rapid trait shifts that offer new avenues for diversification—particularly in systems where traditional genetic adaptation may be (too) slow. To navigate the biodiversity crisis, future research must focus on when ecological opportunity emerges under Anthropocene conditions, and how it can be leveraged. A revised framework must therefore integrate realized–fundamental niche dynamics, ecological–evolutionary timescales, and microbiome-mediated plasticity. Such a framework does not replace evolutionary theory but builds upon it to reflect the multilayered and nonlinear nature of adaptation and diversification in a rapidly changing world. Recognizing these dynamics is essential for informing conservation, guiding restoration, and ultimately sustaining the evolutionary processes that underlie biodiversity itself.

References

1. Wellborn, G. A. & Langerhans, R. B. Ecological opportunity and the adaptive diversification of lineages. *Ecol. Evol.* **5**, 176–195 (2015).
2. Schluter, D. The ecology of adaptive radiation. Preprint at https://doi.org/10.1093/oso/9780198505235.001.0001 (2000).
3. Gillespie, R. Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**, 356–359 (2004).
4. Kassen, R., Llewellyn, M. & Rainey, P. B. Ecological constraints on diversification in a model adaptive radiation. *Nature* **431**, 984–988 (2004).
5. Simpson, G. G. *Tempo and Mode in Evolution*. (Columbia University Press, New York, NY, 1984).
6. Erwin, D. H. Was the Ediacaran–Cambrian radiation a unique evolutionary event? *Paleobiology* **41**, 1–15 (2015).
7. Smith, F. A. *et al.* The evolution of maximum body size of terrestrial mammals. *Science* **330**, 1216–1219 (2010).
8. Steffen, W. *et al.* The anthropocene: from global change to planetary stewardship. *Ambio* **40**, 739–761 (2011).
9. Subramanian, M. Humans versus Earth: the quest to define the Anthropocene. *Nature* **572**, 168–170 (2019).
10. Fischer, E. M., Sippel, S. & Knutti, R. Increasing probability of record-shattering climate extremes. *Nat. Clim. Chang.* **11**, 689–695 (2021).
11. Díaz, S. *et al.* Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* **366**, eaax3100 (2019).

12. Rull, V. Biodiversity crisis or sixth mass extinction?: Does the current anthropogenic biodiversity crisis really qualify as a mass extinction?: Does the current anthropogenic biodiversity crisis really qualify as a mass extinction?: Does the current anthropogenic biodiversity crisis really qualify as a mass extinction? *EMBO Rep.* **23**, e54193 (2022).
13. Barnosky, A. D. *et al.* Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011).
14. Ceballos, G., Ehrlich, P. R. & Dirzo, R. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. U. S. A.* **114**, E6089–E6096 (2017).
15. Winder, M. & Schindler, D. E. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* **85**, 2100–2106 (2004).
16. Bell, G. *et al.* Trophic structure modulates community rescue following acidification. *Proc. Biol. Sci.* **286**, 20190856 (2019).
17. King, R. B., Ray, J. M. & Stanford, K. M. Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. *Can. J. Zool.* **84**, 108–115 (2006).
18. Elliott, B. *et al.* Pollen diets and niche overlap of honey bees and native bees in protected areas. *Basic Appl. Ecol.* **50**, 169–180 (2021).
19. Dirzo, R. *et al.* Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
20. Hallmann, C. A. *et al.* More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* **12**, e0185809 (2017).
21. Bowler, D. E., Heldbjerg, H., Fox, A. D., de Jong, M. & Böhning-Gaese, K. Long-term declines of European insectivorous bird populations and potential causes.

393 *Conserv. Biol.* **33**, 1120–1130 (2019).
394 22. Santangelo, J. S., Rivkin, L. R. & Johnson, M. T. J. The evolution of city life. *Proc.*
395 *Biol. Sci.* **285**, 20181529 (2018).
396 23. Exposito-Alonso, M. *et al.* Genetic diversity loss in the Anthropocene. *Science* **377**,
397 1431–1435 (2022).
398 24. Rocha, R. *et al.* Design matters: An evaluation of the impact of small man-made
399 forest clearings on tropical bats using a before-after-control-impact design. *For.*
400 *Ecol. Manage.* **401**, 8–16 (2017).
401 25. Peters, B., Keller, A. & Leonhardt, S. D. Diets maintained in a changing world:
402 Does land-use intensification alter wild bee communities by selecting for flexible
403 generalists? *Ecol. Evol.* **12**, e8919 (2022).
404 26. Morgan, R., Finnøen, M. H., Jensen, H., Pélabon, C. & Jutfelt, F. Low potential for
405 evolutionary rescue from climate change in a tropical fish. *Proc. Natl. Acad. Sci. U.*
406 *S. A.* **117**, 33365–33372 (2020).
407 27. Bell, G. & Gonzalez, A. Evolutionary rescue can prevent extinction following
408 environmental change. *Ecol. Lett.* **12**, 942–948 (2009).
409 28. Lindsey, H. A., Gallie, J., Taylor, S. & Kerr, B. Evolutionary rescue from extinction is
410 contingent on a lower rate of environmental change. *Nature* **494**, 463–467 (2013).
411 29. Brodie, J. F. *et al.* Secondary extinctions of biodiversity. *Trends Ecol. Evol.* **29**,
412 664–672 (2014).
413 30. Palmer, T. M. *et al.* Breakdown of an ant-plant mutualism follows the loss of large
414 herbivores from an African savanna. *Science* **319**, 192–195 (2008).
415 31. Toby Kiers, E., Palmer, T. M., Ives, A. R., Bruno, J. F. & Bronstein, J. L. Mutualisms

in a changing world: an evolutionary perspective: Mutualism breakdown. *Ecol. Lett.* **13**, 1459–1474 (2010).

32. Becks, L., Gaedke, U. & Klauschies, T. Emergent feedback between symbiosis form and population dynamics. *Trends Ecol. Evol.* **40**, 449–459 (2025).
33. Valido, A., Rodríguez-Rodríguez, M. C. & Jordano, P. Honeybees disrupt the structure and functionality of plant-pollinator networks. *Sci. Rep.* **9**, 4711 (2019).
34. Iwasaki, J. M. & Hogendoorn, K. Mounting evidence that managed and introduced bees have negative impacts on wild bees: an updated review. *Curr. Res. Insect Sci.* **2**, 100043 (2022).
35. Newbold, T. *et al.* Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLoS Biol.* **16**, e2006841 (2018).
36. Calvin, K. *et al. IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland*. http://dx.doi.org/10.59327/ipcc/ar6-9789291691647 (2023) doi:10.59327/ipcc/ar6-9789291691647.
37. Laurance, W. F. *et al.* A global strategy for road building. *Nature* **513**, 229–232 (2014).
38. Coumou, D. & Rahmstorf, S. A decade of weather extremes. *Nat. Clim. Chang.* **2**, 491–496 (2012).
39. Haddad, N. M. *et al.* Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).

40. Fugère, V. *et al.* Community rescue in experimental phytoplankton communities facing severe herbicide pollution. *Nat. Ecol. Evol.* **4**, 578–588 (2020).
41. Kalisz, S., Vogler, D. W. & Hanley, K. M. Context-dependent autonomous self-fertilization yields reproductive assurance and mixed mating. *Nature* **430**, 884–887 (2004).
42. Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* **12**, 184–195 (2009).
43. Salinas, S., Irvine, S. E., Schertzing, C. L., Golden, S. Q. & Munch, S. B. Trait variation in extreme thermal environments under constant and fluctuating temperatures. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **374**, 20180177 (2019).
44. Voolstra, C. R. & Ziegler, M. Adapting with microbial help: Microbiome flexibility facilitates rapid responses to environmental change. *Bioessays* **42**, e2000004 (2020).
45. Keane, R. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* **17**, 164–170 (2002).
46. Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011).
47. Uecker, H., Otto, S. P. & Hermisson, J. Evolutionary rescue in structured populations. *Am. Nat.* **183**, E17–35 (2014).
48. Carlsson, N. O. L., Jeschke, J. M., Holmqvist, N. & Kindberg, J. Long-term data on invaders: when the fox is away, the mink will play. *Biol. Invasions* **12**, 633–641 (2010).

49. Paine, R. T. Food web complexity and species diversity. *Am. Nat.* **100**, 65–75 (1966).
50. Pringle, R. M. *et al.* Predator-induced collapse of niche structure and species coexistence. *Nature* **570**, 58–64 (2019).
51. Henriques, G. J. B. & Osmond, M. M. Cooperation can promote rescue or lead to evolutionary suicide during environmental change. *Evolution* **74**, 1255–1273 (2020).
52. Fontaine, S. S., Mineo, P. M. & Kohl, K. D. Experimental manipulation of microbiota reduces host thermal tolerance and fitness under heat stress in a vertebrate ectotherm. *Nat. Ecol. Evol.* **6**, 405–417 (2022).
53. Hermann, R. J. & Becks, L. Change in prey genotype frequency rescues predator from extinction. *R. Soc. Open Sci.* **9**, 220211 (2022).
54. Hoffmann, J., Hogle, S., Hiltunen, T. & Becks, L. Temporal changes in the role of species sorting and evolution determine community dynamics. *Ecol. Lett.* **28**, e70033 (2025).
55. Porter, S. D. & Savignano, D. A. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* **71**, 2095–2106 (1990).
56. Mooney, H. A. & Cleland, E. E. The evolutionary impact of invasive species. *Proc. Natl. Acad. Sci. U. S. A.* **98**, 5446–5451 (2001).
57. Bøhn, T., Amundsen, P.-A. & Sparrow, A. Competitive exclusion after invasion? *Biol. Invasions* **10**, 359–368 (2008).
58. Röthig, T., Ochsenkühn, M. A., Roik, A., van der Merwe, R. & Voolstra, C. R. Long-term salinity tolerance is accompanied by major restructuring of the coral bacterial

microbiome. *Mol. Ecol.* **25**, 1308–1323 (2016).

59. Moeller, A. H. *et al.* The lizard gut microbiome changes with temperature and is associated with heat tolerance. *Appl. Environ. Microbiol.* **86**, (2020).

60. Janson, E. M., Stireman, J. O., 3rd, Singer, M. S. & Abbot, P. Phytophagous insect-microbe mutualisms and adaptive evolutionary diversification. *Evolution* **62**, 997–1012 (2008).

Funding: This research was financially supported by the Gordon and Betty Moore Foundation (Grant 9196; https://doi.org/10. 73 37807/GBMF9196) awarded to Lutz Becks.

Competing interests: The authors declare no competing interests.

Author Contribution: CV, RH, HS, AK, LB wrote the manuscript.