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Review

Overcoming biotic homogenization in ecological restoration

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Extensive evidence shows that regional (gamma) diversity is often lower across restored landscapes than in reference landscapes, in part due to common restoration practices that favor widespread species through selection of easily-grown species with high survival and propagation practices that reduce genetic diversity. We discuss approaches to counteract biotic homogenization, such as reintroducing species that are adapted to localized habitat conditions and are unlikely to colonize naturally; periodically reintroducing propagules from remnant populations to increase genetic diversity; and reintroducing higher trophic level fauna to restore interaction networks and processes that promote habitat heterogeneity. Several policy changes would also increase regional diversity; these include regional coordination amongst restoration groups, financial incentives to organizations producing conservation-valued species, and experimental designations for rare species introductions.

Highlights

Anthropogenic activities are leading to biotic homogenization.

Common ecological restoration practices often contribute, rather than counteract biotic homogenization at the species, functional, and phylogenetic levels.

It is important to think critically about how to integrate individual restoration projects to most effectively conserve regional biodiversity.

We offer several recommendations to improve restoration practices and policies to increase gamma-diversity in order to maintain ecosystem resilience in a changing world.

Biotic homogenization in restored landscapes

Extensive evidence shows that anthropogenic activities are leading to **biotic homogenization** (see Glossary). Namely, lower **alpha-diversity** (within-site) and **beta-diversity** (increased compositional **similarity** across sites) have led to a reduction in **gamma-diversity** (regional) over time (e.g., [1–4]). In general, anthropogenic impacts such as climate change, fragmentation, and altered disturbance regimes create abiotic and biotic filters that select for overlapping and similar traits that lead to biological simplification [5–7]. The ‘winner’ species comprise both widespread, native generalists and invasive, non-native species that readily disperse and grow rapidly; are commensal with humans; and thrive in disturbed environments [1,8,9]. These species outcompete and often have complex trophic effects on more specialized, endemic, and rarer native species [10,11]. Hence, biotic homogenization has clear implications for both biodiversity conservation and human wellbeing, since ‘loser’ species may play critical roles for provisioning ecosystem services [9]. Ultimately, this homogenization process will likely compromise landscape functionality and undermine the potential of both ecosystems and humans to thrive in a changing environment.

Ecological restoration has been suggested as a strategy to increase biological diversity and overcome the trend towards biotic homogenization at the landscape scale [12,13]. Although there has been extensive debate about the endpoint of restoration efforts in a rapidly changing climate and recognition that restorative activities are undertaken with a wide variety of goals, many restoration projects are motivated by the broad intention of ‘reconstructing’ [14] or ‘rewilding’ [15,16] native ecosystems to recreate the processes, functions, structure, and composition of a native reference system. If restoration practices reintroduce a genetically and compositionally diverse suite of species, including those that are rare and at risk of extinction, this could transform restoration into a powerful tool to reverse biotic homogenization in human-modified landscapes [17]. However, most restoration projects set objectives based on overall cover or abundance of native species and within-site species richness (alpha-diversity) [18,19],

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rather than considering compositional similarity across sites (beta-diversity) and whether the full suite of regional species (gamma-diversity) is re-establishing.

Here we demonstrate that, despite good intentions, ecological restoration efforts often contribute to, rather than counteract, biotic homogenization and discuss the reasons that lead to this trend. We propose strategies to encourage the restoration of broader taxonomic, functional, and genetic diversity across restored sites in the context of regional landscape, including both restored and remnant sites. It is important to think critically beyond individual restoration projects to the broader issue of regional conservation as we embark on the UN Decade on Ecosystem Restoration and restored sites become an increasing portion of human-dominated landscapes. At the same time, we recognize the tradeoffs between increasing gamma-diversity, meeting multiple stakeholder goals, and maximizing the area restored with limited funding.

The evidence

Numerous studies from throughout the world report that even when restoration projects succeed in achieving native species abundance and richness targets, they often are dominated by a subset of the regional species pool that naturally regenerates in or is commonly reintroduced to restored sites (Table 1). For instance, Sapkota *et al*. [20] found that stem-density of woody plants was similar in restored and reference forest stands in Nepal, but beta- and gamma-diversity were higher in reference forests due to the dominance of a single planted, native species (sal tree, *Shorea robusta*) across multiple restored sites. Likewise, Hayward, *et al*. [21] reported that beta-diversity was greater across unlogged dipterocarp forest in Borneo than among either naturally regenerated or actively restored post-logging sites. Conversely, rarer, less-competitive, and highly specialized species are often lacking from restored sites, as compared with nearby reference ecosystems [22–25]. There are, however, exceptions to this trend [12,26].

The species that commonly establish and proliferate in restoration sites typically have traits favored by disturbance. These include adaptations to reproduce large numbers of offspring, disperse widely, and spread asexually; to grow quickly when light, water, and nutrient resources are abundant; and to tolerate cohabiting with humans and the stressors associated with anthropogenic activities [1,8,27,28]. This results in lower diversity of **functional traits** across many restored sites as compared with reference systems [29,30]. For example, D'Astous *et al*. [31] reported that restored peatlands had a narrower range of traits related to flood tolerance and lower average seed mass than remnant sites.

Table 1. Examples[a] of different types of biotic homogenization in restored sites

Type of homogenization	Examples	Refs
Lack of rare, specialized, or endangered species	Temperate forest and grassland plants, grassland moths, wetland algae	[22–24,96]
Low gamma-diversity across restoration sites	Grassland bees and plants, multiple tropical forest taxa	[2,21,24,25] (Box 1)
Predominance of certain functional traits	Peatland plants, tropical forest dung beetles, stream invertebrates, tropical forest trees	[29–31,56]
Phylogenetic homogeneity	Tropical forest and grassland plants, tropical forest birds	[32–34]
Lack of genetic diversity	Mangrove forest, tropical forest birds, greenhouse plants	[36,37,57]
Trophic downgrading	Terrestrial and stream invertebrates, tropical forest birds	[28,44,97]

[a] These are illustrative examples of different types of biotic homogenization rather than a systematic literature review.

Glossary

Alpha-diversity: the species diversity of a relatively small area. For the purposes of this review, it refers to diversity in a single restoration project or study site.

Beta-diversity: the component of gamma-diversity that accumulates as a result of differences between sites. Includes heterogeneity resulting from stochastic variation within a single habitat and differences between habitats along environmental gradients.

Biotic homogenization: the replacement of high-diversity biotas by low diversity and more similar biotas.

Ecological restoration: the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed.

Functional traits: the ecological attributes of a species that relate to dispersal, survival, capture of resources, and the effect of that species on the overall pool of resources in the ecosystem.

Gamma-diversity: the number of species found across a relatively large area. It is the product of alpha- and beta-diversity. For the purposes of this review, gamma-diversity corresponds to the diversity of a landscape or an ecoregion.

Habitat: variations of an ecosystem along abiotic gradients that support different species compositions. For example, California grassland composition differs as a function of soil type (e.g., serpentine grasslands) and soil moisture (e.g., wet meadows).

Similarity: (also compositional similarity); a metric of how much the species composition of two or more sites overlap.

Given that functional traits are often conserved phylogenetically, it is not surprising that several studies also report lower phylogenetic diversity in restored than reference sites [32,33]. Cosset and Edwards [34] found the avifaunal community in restored sites had lower phylogenetic and functional diversity than remnant sites. Turley and Brudvig [35] reported that savanna restoration in former agricultural lands in the southeastern US improved phylogenetic diversity, but not to the level in reference systems.

Likewise, a growing body of evidence suggests that restored sites often host lower genetic diversity than reference systems ([36,37] but see [38,39]), particularly of species with small populations and those that are propagated clonally [40]. This trend is consistent with a recent meta-analysis that showed that *ex situ* plant populations, which often serve as the source for vegetative material for restoration, have lower genetic diversity than wild populations; this is due both to practitioners not collecting across the full species range and to genetic erosion over time [41]. This pattern is highly concerning given that maintaining and increasing genetic variability is key to species adjusting to rapidly changing climatic conditions [42,43].

Several studies also demonstrate that restored sites tend towards trophic downgrading and simplification of species interaction networks, as a result of reduction or absence of top-level predators and species with specialized mutualisms in restored sites (Table 1). Tullos *et al*. [28] found more macroinvertebrate shredders in reference streams and a greater abundance of collector-gatherers in restored streams, indicating trophic downgrading. Likewise, trophic levels and body sizes of birds were lower in restored compared with reference montane forests in Rwanda due to the absence of raptors and large-bodied frugivores and invertivores [44].

What is less clear is whether gamma-diversity will increase or decrease over time across restored sites given the paucity of long-term, multi-site restoration studies. Classic forest succession models predict that a more diverse suite of **habitat** specialists will disperse to and establish in restored sites over time, but the few long-term, multi-site restoration studies show that this does not necessarily happen [22,45,46] (Box 1). Moreover, restoration typically occurs in fragmented habitats with strong edge effects that favor invasive species [47] and recurring anthropogenic disturbance [48], thereby leading to positive feedbacks towards homogenization. Finally, in some cases, recently restored areas may create suitable habitat for rare and threatened disturbance-dependent species in landscapes with limited early-successional habitat and thereby increase gamma-diversity [12,49].

Causes of biotic homogenization in restoration

Local and landscape context

These patterns of species, functional, and genetic homogenization in restored sites can be explained by various factors. To start, conditions both within and in the landscape surrounding restored sites favor biotic homogenization. By default, restored sites have a history of disturbance, which selects for disturbance-adapted native species and invasive, non-native species that are strong dispersers and competitors and, in turn, promotes homogenization. Moreover, restoration sites often lack the within-site abiotic heterogeneity (e.g., microtopography, soil moisture) that provides a range of niches for different species [50,51].

Restored sites are often embedded in landscapes where remnant habitats are highly fragmented and affected by anthropogenic impacts (e.g., selective logging, hunting, influx of agricultural chemicals), which results in biotic homogenization of the species pools available to colonize restored sites [2,9,52]. The abundance of generalist native and invasive non-native species in most fragmented landscapes, combined with the typically strong dispersal abilities of these species, means that they are highly likely to be the 'winners' [9,53] (Figure 1B). For example,

Box 1. Biotic homogenization in restored California coastal prairies

California coastal prairies are the most species-rich grassland type in North America, but common restoration practices typically do not aim to restore the full suite of possible species. Lesage *et al*. [55] reported that practitioners recognized the conservation value of less commonly used species but did not plant them due to risk-aversion and concerns about meeting compliance standards. Luong (J.C. Luong, Doctoral dissertation, University of California Santa Cruz, 2022) further addressed this question by measuring vegetation composition and conducting land manager surveys of 37 restored coastal prairies. The sites ranged in age from 3 to 30 years post-implementation and spanned a 1000-km north–south climate gradient in coastal California. They found that nearly 50% of practitioners plant the same four perennial grass species (Figure I), despite the fact that coastal grasslands host over 400 native species, many of which are annual forbs. Some practitioners indicated use of both widespread and less-common species if they already felt confident in achieving their project targets. Practitioners preferentially selected perennial bunchgrasses because they are competitive and easy to establish with limited resources. These results suggest that current restoration practices are leading to taxonomic biotic homogenization of coastal grasslands and a lack of recovery for regionally rarer species.

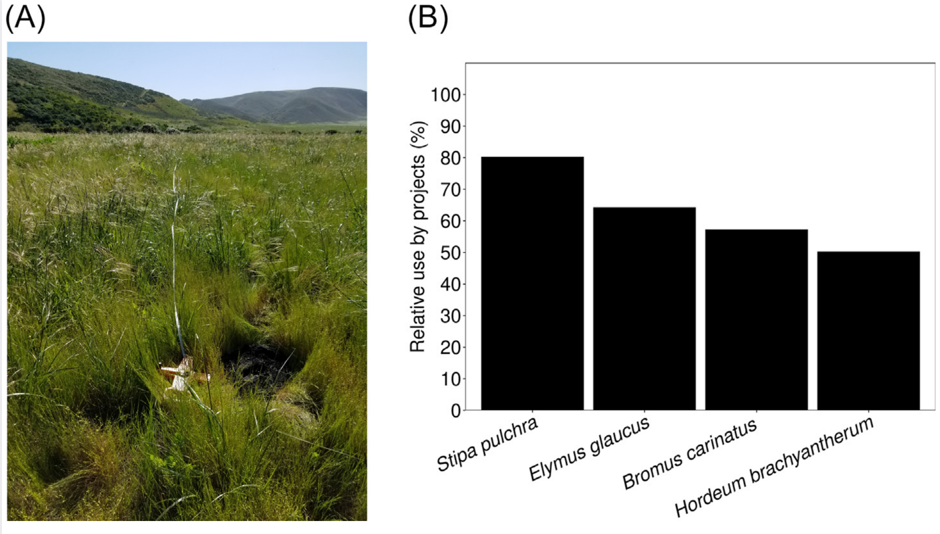

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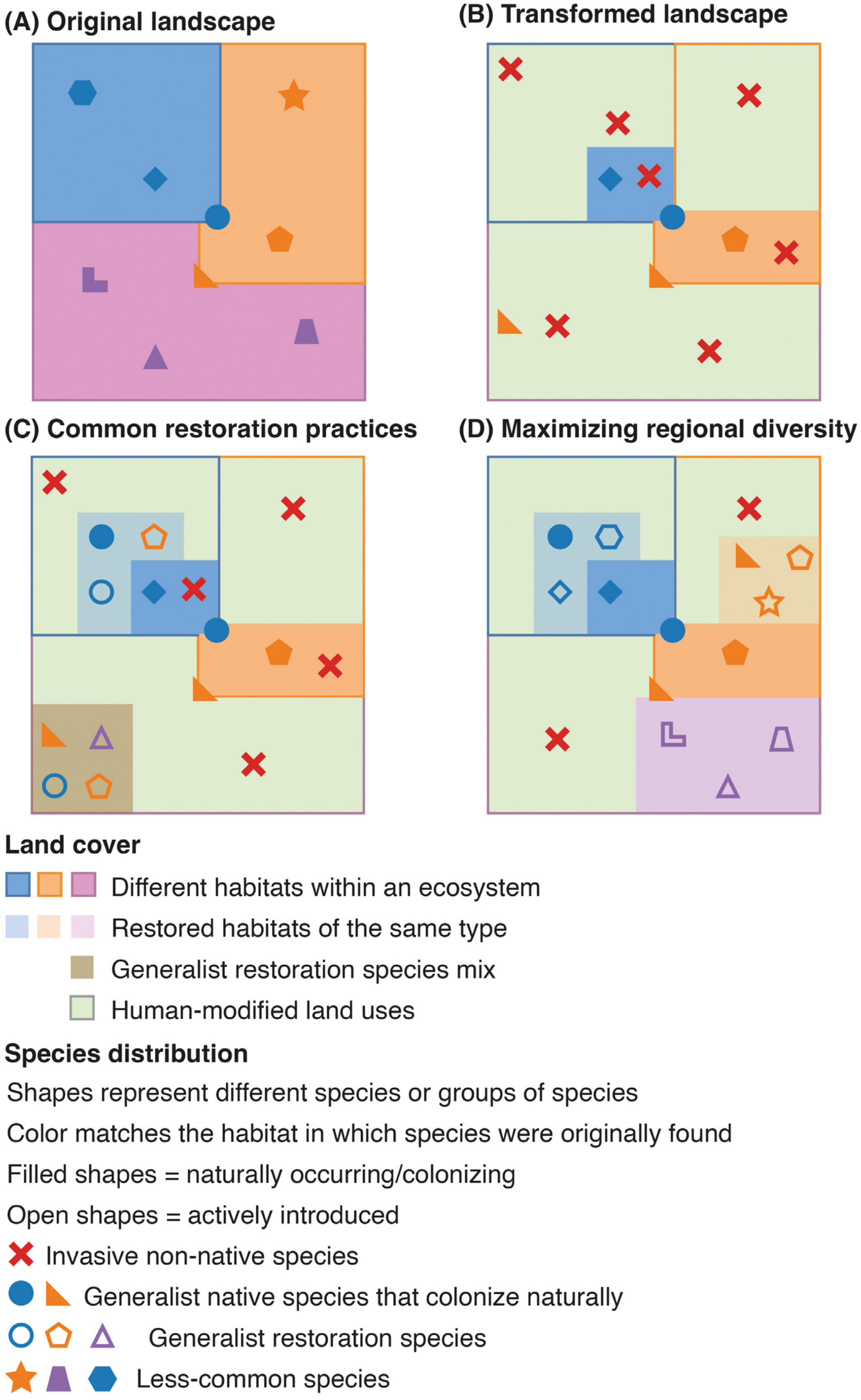
Figure I. (A) Restored coastal prairie dominated by one perennial grass, *Stipa pulchra*, a species that is commonly planted along the entire California coast. (B) Percentage of projects in which the most commonly used species were planted; practitioners preferentially selected these species because they have high survival or growth.

habitat fragmentation and defaunation in tropical forests has led to a paucity of fauna capable of dispersing large seeded, later-successional tree species [54].

Restoration actions

In addition to local and landscape conditions, some commonly employed restoration practices promote biotic homogenization. These practices stem from practical, economic, and legislative constraints. First, despite the fact that species composition varies across abiotic gradients (i.e., habitats) within an ecosystem (Figure 1A), practitioners often reintroduce the same species at multiple sites across the landscape (Figure 1C). Commonly used species typically are cheap and easy to propagate; have well-established collection, propagation, and reintroduction methods; and have a record of establishing well [55] (Figure 1C). This reduces project costs and increases the likelihood of achieving restoration objectives. In some cases, these are the same widespread native generalist species that establish naturally (Figure 1C). Luong *et al*. (Box 1) found that practitioners introduced a similar subset of perennial grass species in 37 grassland restoration projects spanning 1000 kilometers along the California coast. Moreover, the only



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commonly reintroduced forb species is yarrow (*Achillea millefolium*), a circumboreally distributed perennial species that colonizes naturally through both seed dispersal and vegetative spread. Brancalion *et al*. [56] reported that nurseries in southeastern Brazil lacked large-seeded, later-successional trees due to the high cost of propagating these species, despite their ecological importance.

Second, restoration nurseries are under pressure to produce large quantities of seeds and plants to meet the growing demand, which encourages collecting seed and vegetative material from the largest, most productive plants at the peak time of plant maturation, which can lead to genetic homogenization [56–58]. In addition, nurseries may not be allowed to collect seeds in protected areas, often a major repository of rare, specialized species [59], and it can be challenging or impossible to collect species that are legally protected due to complicated and costly permitting procedures. As a result of the high demand for seed to scale-up restoration, plants of short-lived species are often grown in the greenhouse or on seed farms to increase the amount of seed. However, multiple cycles of farm- or greenhouse-grown seeds for restoration use can result in reduced genetic diversity and plant fitness, as compared with wild populations [57,58,60].

Finally, terrestrial restoration projects largely focus on reintroducing plants rather than fauna, fungi, and microbial communities, in part because it is challenging to reintroduce larger predatory fauna [61] and other species with complex mutualistic interactions [62]. This favors the reintroduction of generalist and lower-trophic level species, simplifies interaction networks in restored sites, and can have cascading effects on regional diversity [61,63]. For example, Walsh *et al*. [64] assert that it would be extremely challenging to restore the endangered Hawaiian succulent lobelia (vulcan palm, *Brighamia insignis*) due to lack of visitation by specialized hawkmoth pollinators.

The tendency towards using easy and tried-and-true species is understandable given the need for practitioners to meet restoration targets, particularly for projects that are legally mandated and do not receive financial incentives to cover the additional costs involved in the production of conservation-valued species. For example, Lesage *et al*. [55] found that, due to both cost and risk aversion, grassland restoration practitioners in California preferentially used competitive perennial species, rather than including the annual forb species that comprise a large proportion of California grassland plant diversity. Annual plant populations fluctuate dramatically from year to year, making it challenging for practitioners to achieve restoration targets when using annual species. In addition, using harder to propagate and slower growing species will likely reduce survival and delay the structural recovery of the ecosystem, which may increase maintenance costs. Reintroducing vertebrate fauna can be extremely expensive, require large areas, and be socially controversial [65].

Recommendations to improve gamma-diversity

Proactive planning is essential for restoration efforts to succeed in the promise of counteracting biotic homogenization and restoring all aspects of biological diversity across the landscape. We suggest a number of restoration practices and policies that will help to achieve this end

Figure 1. Counteracting biotic homogenization of plants in restored landscapes.

For a Figure360 author presentation of Figure 1, see https://doi.org/10.1016/j.tree.2022.05.002.

(A) Original landscape in which habitats with different species compositions are distributed across abiotic gradients (e.g., moisture, soil type) within an ecosystem type (e.g., coastal grassland, tropical forest). (B) Landscape transformed by land conversion to anthropogenic uses (e.g., agriculture) results in habitat fragmentation, biotic homogenization, and the spread of invasive, non-native species and generalist, native species. (C) Common restoration practices in which a similar, generalist restoration species mix is planted throughout the landscape. (D) Restoration aimed at maximizing gamma-diversity by prioritizing locations that enhance connectivity (restored habitats adjacent to remnants), matching species compositions to the original abiotic conditions, planting less-common species that rarely colonize naturally, and making more extensive efforts to control invasive species in restored habitat.

(Box 2). We acknowledge that many of these practices will increase the costs of restoration and, as such, will require careful consideration of trade-offs between maximizing the area restored versus the regional biodiversity conserved.

First, restoration sites that are located near or facilitate connectivity with source populations of flora and fauna should be prioritized to maximize both the taxonomic and genetic diversity of colonizing species, minimize edge effects, and enhance connectivity with hydrologic processes [37,66–68] (Figure 1D). The development and application of novel remote-sensing and analytical techniques have greatly enhanced the capacity to select sites that maximize connectivity and to monitor the restoration of biodiversity at large spatial scales [69,70]. Of course, the feasibility of maximizing connectivity depends on the extent and quality of remnant habitat in the landscape, as well as land ownership and the amount of fungibility amongst potential restoration sites.

Second, restoration should be designed to provide sufficient habitat heterogeneity both within and among sites to provide niches for a range of species. This is done most effectively by restoring the

Box 2. Recommendations for overcoming biotic homogenization in restoration

Site selection and protection

- Prioritize restoration sites near diverse source populations to maximize landscape connectivity
- Favor areas that maximize environmental heterogeneity and thus habitat variability for a diverse suite of native plant and animal species
- Use spatial analysis tools and both field-collected and remotely-sensed data to select sites and map environmental variability
- Protect restoration sites against reconversion to allow time for a diverse suite of species to colonize and establish

Species selection and propagation

- Select species for reintroduction that:
    - are unlikely to colonize naturally
    - are adapted to localized abiotic habitat conditions rather than using primarily widespread, generalist species
    - represent phylogenetic and trait diversity
    - facilitate the colonization of and interactions with other species
- Follow existing guidelines for propagule collection that maximize genetic diversity
- Periodically introduce individuals from wild-collected populations to supplement the genetic diversity of greenhouse- or farm-grown plants and captively-bred fauna
- Improve information sharing about propagation, captive breeding, reintroduction, and maintenance methods, particularly in widely accessible online formats
- Create programs to exchange genetic material amongst organizations (e.g., nurseries, zoos), thereby maximizing diversity without each organization having to collect all species or as many individuals of a single species

Restoration interventions

- Restore historic abiotic heterogeneity within habitats
- Re-establish historic disturbance regimes that create habitat heterogeneity
- Control invasive species and in some cases widespread, generalist native species that inhibit the establishment of a diversity of native species
- Reintroduce later-successional species after habitat conditions are more suitable
- Consider the mosaic of resources and habitat features that are required for faunal movement, foraging, and reproduction
- Increase reintroductions of fauna to restore species interaction networks

Policies

- Coordinate restoration species selection regionally across different land management organizations to maximize gamma-diversity
- Include requirements for the use of some less-common species in restoration regulations
- Provide financial incentives to groups producing and reintroducing conservation-valued species
- Include species composition measurements as part of restoration monitoring frameworks
- Budget sufficient funding for long-term monitoring and adaptive management
- Allow experimental designations to allow for trial introductions of rarer species
- Provide access to sources of propagules of rare and specialized species

natural processes and disturbance regimes (e.g., channel meandering, fire, large ungulate grazing) that create heterogeneous habitat conditions [16]. In cases where this is not possible, it may be necessary to actively restore small-scale topographic heterogeneity to concentrate nutrient and water resources [50]. The plant species reintroduced should be tailored to localized habitat conditions (Box 2, Figure 1D). Restoring habitat heterogeneity for fauna requires specific consideration of the mosaic of habitat types and resources needed for movement, foraging, reproduction, and protection from predators, rather than assuming all restored habitat is equally suitable [63,71].

Third, the suite of species actively introduced to a site must be thoughtfully selected and coordinated regionally (Box 2). We recommend selecting species with a range of traits and phylogenetic diversity, that are adapted to the local habitat conditions, and that will facilitate the colonization of and interactions with other species [15,72–74]. For example, fleshy-fruited tree species serve to attract seed-dispersing birds for tropical forest restoration [75]. Likewise, reintroducing faunal species can restore ecological processes and habitat heterogeneity. For example, reintroduction of the giant Galapagos tortoise (*Chelonoidis hoodensis*) has reinitiated seed dispersal and increased the recruitment of juvenile plants of the endangered tree cactus, *Opuntia megasperma* var. *megasperma* [76]. Whereas many restoration projects primarily reintroduce early-successional, disturbance-adapted plant species, more effort should be focused on reintroducing those species that are less likely to colonize naturally (Figure 1D) and ideally introducing them later in restoration once site conditions are more favorable for their establishment [77,78].

Diversifying the suite of actively reintroduced plant and animal species will require further research on how to propagate and reintroduce less common species and potentially financial incentives to those that produce them, particularly in highly diverse systems [56]. Equally important is improving the sharing of this information, which is often passed on verbally through informal communications amongst restoration practitioners. Recently, some online, open access portals have been developed to share information more broadly about plant selection and propagation, which can serve as models (e.g., [79], see Table 3 in [80], http://data.kew.org/sid/]. For example, the Diversity for Restoration free online tool was originally developed for tropical dry forest trees of Colombia and is being expanded to other countries; the tool combines habitat suitability maps now and under future climate conditions, functional trait and phylogenetic information, and local ecological knowledge to guide selection of species and seed sources tailored to habitat conditions and project goals [80]. In addition, trait data for many plant species are available on the TRY database (https://www.try-db.org/TryWeb/Home.php), facilitating their incorporation in plant species selection.

Fourth, recent studies show that restoration efforts can be successful in improving genetic diversity when pursued with intentionality [60,81]. This requires following existing, best-practices guidelines for collecting plant materials, such as collecting from a minimum number of individuals and populations, across the temporal and spatial range of where species reproduce, and from both small and large individuals, as well as keeping detailed records of where and when the seeds were collected [60,82,83]. It is also important to continue to collect from wild populations over time to maintain genetic diversity, following best practices to minimize impacts on the source populations, rather than solely relying on seed farms or captively bred faunal populations [58,59]. Initiatives such as the Ecological Restoration Alliance of Botanic Gardens [84] contribute to coordinating the supply of conservation-valued species to restoration projects and trading seeds amongst groups to increase genetic diversity among *ex situ* collections.

Fifth, restoration projects must be protected and maintained for the long-term to allow for the colonization and establishment of suitable habitat for a diverse suite of species over time. The specific ongoing maintenance activities needed will depend on the ecosystem and site conditions. Reintroducing rarer and later-successional species once suitable habitat conditions have developed is more successful in some ecosystems [85,86], but is challenging given the short timeline of many restoration projects. In ecosystems that have evolved with specific natural disturbances and host a diversity of disturbance-dependent species (e.g., chaparral: fire; riparian forests: flooding), maintaining a disturbance regime and mosaic of habitat stages will be key to maximizing gamma-diversity. In many ecosystems, ongoing invasive species removal will be necessary to maintain and enhance gamma-diversity.

Implementing these recommendations will require modifying restoration targets, financing, and regulations. Most restoration compliance targets focus on cover, abundance, or alpha-diversity, rather than regional-scale diversity. These site level requirements are necessary, but should be complemented with regional coordination of restoration efforts to maximize gamma-diversity at a landscape scale. For example, the Atlantic Forest Pact, a group of over 270 business, government, academic, and non-profit groups that aims to restore 15 million hectares of Brazilian Atlantic forest, has worked together to coordinate research efforts and share information that have supported the propagation of over 150 tree species within individual forest nurseries [87] (Box 3). Projects that include restoration of rarer species and habitats could be prioritized for funding from public sources, such as the US Wetland Reserve Program (now part of the Agricultural Conservation Easement Program: https://www.landcan.org/local-resources/Agricultural-Conservation-Easement-Program-ACEP/35602) which provides a 50–75% cost-share to farmers and ranchers who restore wetlands on their land. Likewise, increasing gamma-diversity might be part of countrywide restoration policies, such as the recently issued Chinese National Guidelines for restoration [88] and other similar efforts that are underway as part of the UN Decade on Ecosystem Restoration. Additionally, policies for compliance projects, especially those driven by biodiversity offsetting policies, should require that projects incorporate at least a few native species that are part of the regional species pool but not commonly used in restoration. Quite often, such policies focus on a narrow suite of biodiversity and fail to minimally compensate for the destruction of native ecosystems [89].

To alleviate restoration practitioners' concerns about using poorly tested species, regulations should include research designations to allow for testing new methods and species. For example, under the US Endangered Species Act, reintroduced populations can be designated as 'experimental' to allow for research on how to most successfully establish and grow species without increasing landowner liability. In addition, regulations should allow seed collectors to responsibly access rare and legally protected species and botanical gardens to establish seed orchards with these species.

Concluding remarks

The UN Decade on Ecosystem Restoration and other related initiatives have lofty goals for restoring biodiversity and associated ecosystem services and improving human livelihoods. Achieving these goals, however, will not be easy. Realizing the full potential of restoration to counteract biotic homogenization will require additional research on strategies to increase the recovery of gamma-diversity, as well as longer-term, multi-site studies to compare the outcomes of such efforts over time (see Outstanding questions). Indeed, mimicking the complex and long-term processes of species assembly comprises a major scientific challenge [90]. Moreover, we need to work toward feasible and effective policies to restore gamma-diversity and further promote regional collaboration, rather than competition, among restoration initiatives operating in the same landscape.

Equally, if not more difficult, will be evaluating critical trade-offs between maximizing the area restored; meeting the needs of local stakeholders, and the additional costs, labor, and time needed to undertake actions to enhance regional biodiversity; and identifying synergies to meet

Outstanding questions

How much does gamma-diversity recover naturally over time?

Does investing additional resources in active restoration increase gamma-diversity beyond simply allowing for natural regeneration?

To what extent will measures to reverse biotic homogenization be undermined by environmental changes?

What are the best strategies to restore the pre-disturbance habitat heterogeneity needed to provide appropriate conditions for the full suite of species?

How do we restore rare species with complex species interactions and maintain them over the long-term?

Does implementing measures to reverse biotic homogenization compromise other restoration goals, such as carbon sequestration, soil protection, and improving human livelihoods?

What is the balance between the increased restoration costs, including long-term maintenance and adaptive management, to increase gamma-diversity and the potential financial benefits resulting from it (e.g., carbon sequestration, pollination, ecotourism)?

Where does one draw the line in how many rarer species to include while balancing restoration budgets?

What policy regulations or incentives are most effective for increasing regional gamma-diversity?

How do we most effectively coordinate species selection for restoration across ecoregions?

Box 3. Increasing gamma-diversity in restoration of the Brazilian Atlantic forest

The Atlantic forest of Brazil is one of the most biodiverse ecoregions of the world with 3263 tree species, of which ~60% are endemic. Restoring such a huge diversity of trees is a major challenge for forest restoration programs and a valuable opportunity to save hundreds of species from extinction. Restoration programs in this region have made use of a relatively high diversity of tree species (Figure I), but the restoration species' pool is composed mostly of a narrow group of species with similar traits. In a large-scale assessment of tree diversity in restoration plantations in the Atlantic Forest, based on 961 restoration projects and more than 14 million seedlings planted, Brancalion *et al*. [56] found that species composition was highly biased towards small-seeded, wind-dispersed, and cheaper seeds. To counteract this under-representation of tree species diversity in restoration programs, several strategies have been established: (i) seed exchange programs among nurseries have been organized, thereby maximizing genetic and species diversity [93]; (ii) legal policies now require a minimum number of native tree species in restoration programs [94]; (iii) capacity-building courses have been organized with seed collectors and local communities [87]; and (iv) spatial prioritization analyses have been used to select areas with greater potential to mitigate species extinctions [69] and maximize landscape connectivity [95], which may promote the arrival of rare and threatened species in restoration sites.

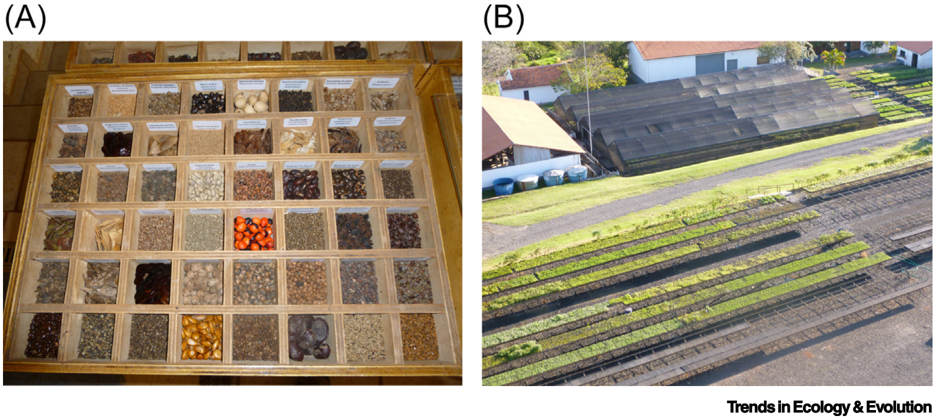

Figure I. (A) Collection of various Atlantic forest tree seeds used for restoration. (B) Large nursery with the capacity to produce ~1 million seedlings annually of a diversity of native species.

multiple goals. A key step in all restoration projects is clearly identifying and agreeing to goals amongst stakeholders so that appropriate methods can be selected [91]. For example, if projects are driven by biodiversity offsets then maximizing biodiversity should be a priority, whereas if forest landscape restoration projects are focused on providing income and food sources to local landholders, introducing a smaller suite of economically and culturally valuable tree species may be a more appropriate strategy. Fortunately, some examples, such as a large-scale forest corridor restoration project in the Pontal do Paranapanema region of Brazil, demonstrate that with careful planning, regional biodiversity, habitat connectivity, and local stakeholder livelihoods can be simultaneously improved [92] (Box 3), though this will not be the case for all projects.

Nonetheless, restoring gamma-diversity is critical to maintaining functioning ecosystems that are resilient to climate change and, ultimately, to achieving most of the benefits that motivate ongoing restoration initiatives. We highlighted causes of biotic homogenization in ecological restoration and recommended potential strategies to overcome them (Box 2). A thoughtful consideration of these mechanisms and application of solutions is now needed as part of an integrated effort among restoration organizations, practitioners, researchers, and policymakers.

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Declarations of interest

No interests are declared.

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