Trends in Ecology and Evolution

Overcoming Biotic Homogenization in Restoration

--Manuscript Draft--

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Abstract:	Extensive evidence shows that regional (gamma) diversity is often lower across restored than 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 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.

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Dear Dr. Stephens,

20 April 2022

I have uploaded a new version of our manuscript "Overcoming Biotic Homogenization in Restoration" (TREE-D-22-00038), which we have revised substantially with the helpful comments from you and the three reviewers.

We have provided detailed responses to all the reviewer comments. As noted in that letter, we plan to make a Figure 360 video for our main figure, and we will do that once you approve the revised figure.

We have replaced the reference to unpublished data in Box 1 with a reference to Mr. Luong's dissertation. Mr. Luong will be submitting his dissertation in early May and we have confirmed with the graduate school at UC Santa Cruz that it will be posted and assigned a DOI within in week, so we anticipate that it will be readily accessible by 15 May 2022.

We appreciate your considering a revised version of the manuscript and look forward to your response.

Sincerely,

Karen D Holl

Karen Holl

Responses to Editor and Reviewers

Editor comments: As you can see from reading the referee reports below, all three Referees were positive about the piece overall. Referee 2 mostly has points of clarification and has identified some places where more explanation is needed. Referee 1 requests a definition of homogenisation - I think what you have is fine. Referee 3 has provided a lot of points to ponder, particularly around beta vs gamma diversity. You may not choose to address them all explicitly in the manuscript. They suggest leaning on Filgueras et al (ref 9) a little more - this would open space for further, more novel, discussion.

Thank you for the helpful guidance to prioritize our revisions. We detail below in italics how we have responded to each reviewer comment. We have also provided a version with the changes tracked.

I have provided a marked up copy of your manuscript with comments and suggestions that I would like you to follow. Major (non-typographical) comments should also be included in your response to reviewers document.

We made the following changes in responses to your comments on the manuscript:

- *We shortened the final paragraph of the introductory section as suggested.*
- *We double checked the italicization of Latin names in the references and checked the reference formatting.*
- *We renamed Table 2 to Box 3.*
- *We moved the indicated Figure 1 caption text directly onto the figure. This has made the figure quite long vertically. If it would be better for page layout, we could move the legend text to the right of the panels so it is landscape layout.*
- *We removed references from the glossary.*

Therefore, I encourage you to prepare a revised version of your article, taking into account the referees' and my suggestions as far as possible - but taking care not to increase the length of the text or reference list beyond that recommended in the instructions to authors. Please also take this time to update your article with any new relevant papers.

We have added a few new references published within the last year (e.g., Hayward et al. 2021, Lane et al. 2022). The revised manuscript is 3500 words and has 98 references.

* You might be interested in contributing a Figure360 video along with your revised manuscript. This optional feature is a narrated, animated version of one of your figures that helps the reader zoom in on the most important take-home message in two minutes or less. The video should contain data and panels from only one figure, with minimal introduction. For further guidelines and examples, please

see https://www.cell.com/figure360. It must be submitted prior to acceptance of your article.

We plan to prepare a video to explain the various concepts illustrated in Figure 1 but will do this once the revised version of the figure has been approved. We realize that this must be submitted prior to final acceptance but it seemed like made more sense to ensure we didn't need to make further revisions to the figure prior to recording the video.

* You are welcome to use either UK or US English *We have used US English.*

* The first time a species is mentioned, both the common name and scientific name should be given. If a common name does not exist for the species, give an indication of what type of organism it is (e.g. nematode, moth). Where possible, do the same for higher taxonomic groups

We ensured that there was a description of the type of organism or common name prior to the Latin name. A few of the tropical species we refer to do not have common names or have many common names in different languages depending on the region.

Reviewers' Comments:

Reviewer #1: This manuscript is a highly readable and insightful review of the problem of biotic homogenization in the context of ecological restoration. The authors clearly define the problem, briefly review the evidence, and propose practical and policy solutions for counteracting homogenization. The review is synthetic and timely, and although the ideas presented are not entirely novel, I am not aware of any existing reviews that bring these ideas together in a single paper. The Highlights and Abstract sections succinctly capture the primary arguments. Overall, the manuscript is clearly written, and I have only minor suggestions for improvement.

We appreciate the positive feedback.

One point that I consider important for framing some of the arguments in the manuscript: the authors never explicitly define homogenization with respect to a specific set of sites. When they write of homogenization that results from restoration, are they thinking of homogenization among a set of restored sites, among a set that includes both restored and naturally occurring sites, or some mix of both depending on the point they are arguing? For example, the statement on line 44, "ecological restoration efforts often contribute to, rather than counteract, biotic homogenization," has different implications if we consider: (A) just restored communities or (B) restored communities plus naturally occurring communities. If the authors intend A, line 44 could imply that even if restored sites are fairly homogenous, restoration could increase heterogeneity (beta diversity) and gamma diversity of a region. If the authors intend B, line 44 could imply that restoration causes net harm - the loss of beta and gamma diversity in a region. Clarity on this point is necessary for interpreting some of the points in the manuscript and for operationalizing the definition of "homogenization" in any future empirical studies that might be inspired by this manuscript.

The reviewer makes good points. We note in lines (106-108) that restoration can add to gamma-diversity in the landscape by providing early-successional habitat. We have also added a sentence that we are considering both (A) and (B) above (lines 46-47). Our recommendations largely focus on how to increase gamma-diversity through restoration, given the focus of our article, but that necessarily has to be considered with the context of the landscape and existing reference sites, a point that we note in a few places in the manuscript.

This is also important to consider in the context of the overall condition of the landscape within which restorations are embedded. For example, the points that the authors make in lines 116-124 support the notion that a degraded landscape context contributes to homogenization among restored sites. However, the conclusion that they seem to draw from this is that, "priority should be given to restoration sites that are located near or facilitate connectivity with source populations" (lines 191-192). I don't disagree with this, and such a strategy might counteract homogenization among restored sites. However, this strategy might not be effective in regions like the US Midwest, with over 99% loss of tallgrass prairies and 85%-90% loss of wetlands. Counteracting regional homogenization (considering all sites) requires restoration within a highly degraded matrix. Even if the restored sites are themselves homogenous, they still "heterogenize" the landscape.

We agree with this comment and have now noted that the degree to proximity to source populations will help to counteract biotic homogenization will depend on whether there are remnant source populations in the landscape (lines 192-193).

18: To me, "harsh abiotic and biotic filters" implies physical stress. However, a major cause of homogenization in plant communities is the alleviation of a physical stress through eutrophication. I suggest replacing "harsh" with a more neutral word - maybe "altered." *Removed “harsh.”*

20: Replace "comprised of" with "comprise" or "composed of." *Changed to “comprise”.*

112: It might be helpful to give a couple of examples of "within-site abiotic heterogeneity" here - microtopography, vertical complexity of the vegetation, etc. *Done.*

251-255: I don't think that the authors intended this, but it almost reads as if they expect predictable increases in diversity if we just give restored sites enough time. Homogenization is a temporal process - restored sites often become more, not less, homogenous through time. Long-term protection is important, but long-term monitoring and continual maintenance are just as important.

All three reviewers made different comments noting that we inadequately addressed the issue of time in biotic homogenization, and we agree. We have expanded and provided a more nuanced discussion of time to note that gamma-diversity can either decrease or increase over time depending on a number of factors. We moved our initial discussion of the temporal component from the "local and landscape context" subheader of "causes of biotic homogenization" where we realized it was out of place. We have reframed the discussion slightly and moved it to the end of the "evidence" section and note that there is minimal and conflicting evidence about how biotic homogenization changes over time in restored sites (lines 99-103). We have expanded our discussion of long-term protection and maintenance in the "recommendations" section (lines 247-256) and note in the conclusions that more multi-site, long-term studies are needed (lines 292-293).

593, 622: The periods at the end of these lines are inconsistent with the other bullet points. *Fixed.*

Outstanding Questions: In the second and fifth bullet points, "reverse" would be more appropriate than "revert." *Corrected.*

Reviewer #2: This article poses a justified critique towards restoration efforts, which may not consider the impacts of species selection sufficiently - this lack of consideration may, instead of increase the diversity of a region, instead foster biotic homogenization. The article requests a better regional coordination of practitioners and more long-term engagement, political and financial support for restoration projects to achieve their full potential, and suggests to move beyond site-specific targets. The well-structured and articulated text compiles a selection of evidence of biodiversity in restored sites not only by considering species richness. It thus widens the scope of measuring restoration success to include also other groups than plants, and to measure restoration success also in terms of trophic networks, phylogenetic diversity and species´ traits. While it should not be surprising that restoration may increase biodiversity, but not result in similar high biodiversity compared to what the natural state of the ecosystem entailed. Notwithstanding, the points raised by the authors deem important to me, and I find the practical recommendations appealing, but suggest a few changes and expansions:

By considering historical occurrences of e.g. rare species and by creating the conditions for their occurrence, automatically the gamma diversity of a region will also be favoured. However, the authors´ point here is that often species are favoured in restoration activities that are easy to grow and that potentially show a quick success. This, of course, undermines the potential of a restoration activity to fully achieve richness beyond alpha diversity, and I support this point. Notwithstanding, restoration projects are often designed to happen over a shorter period of time compared to the natural dynamics that have created conditions which enables the presence of species, specifically those sensitive and slow-growing species that are often not favoured in restoration activities. Thus, the question arises in how far this temporal dimension can be considered in projects and whether the aim of restoration to increase the presence of native species might not already head towards the "right" direction and over a longer term, the gamma diversity will be favoured as well. I would like to encourage an expansion of this temporal component in the setting of active and passive restoration endeavours, which is mentioned in lines 131ff and 252ff. I appreciate that this temporal aspect is already included also in lines 221ff, to distinguish several periods of time in restoration activities. This is also closely tied to the recommendations by the Society for Ecological Restoration: https://www.ser.org/page/SERNews3113

As noted in our response to reviewer 1, we agree with this point and have expanded our discussion of the temporal component of biotic homogenization at both the points in the paper that the reviewer notes.

- Line 4: what are propagation practices? *The definition of "propagation" is "the breeding of specimens of a plant or animal by natural processes from the parent stock." We think the terminology is clear so we didn't change the terminology, particularly since an alternative description would require more words and we are at the word limit for the abstract.*

- L. 5-9: long sentence, suggest to break up. *We have separated the three examples of strategies with semi-colons to provide more of a break between clauses but think that it would result in choppy writing to have individual sentences for each of the examples. Moreover, we are at the word limit for the abstract.*

- L. 9-21: sentence hard to understand: put active verb towards beginning of sentence. *We moved the main verb to the beginning of the sentence and divided this into two sentences.*

- L. 56 ff: Unclear whether this evidence has been compiled through a systematic literature review? *We thought it was clear that we are using illustrative examples rather than a systematic literature review, which would have been challenging given the range of terms used to refer to the different scales of diversity, biotic homogenization, and restoration. We now note in Table 1 that we are using illustrative examples from the literature rather than having conducted a systematic literature review. We did not add a sentence to the text explicitly stating that "this was not a systematic literature review", as we thought that would break up the flow of the text and we are at the word limit. We are willing to add that sentence if desired.*

- L. 107: The following sentence does not make sense to me: "local and landscape conditions in restored sites favour biotic homogenization. *We have rephrased to "both within and in the landscape surrounding restored sites".*

- L. 113: Habitat is, by definition, suitable for the species under consideration. Otherwise it would not be its habitat. Replace the term here and in the following by "ecosystem", "biotope" or "vegetation"? *This is where we define how we use habitat throughout the rest of the paper so we have left the term as written. We agree that it is not a perfect term but do not think the suggested replacement terms would improve the clarity.*

- L. 158: replace "And" at the beginning of the sentence by: "Moreover" (or similar). *Done.*

- L. 212: I miss the recommendation to select those species that suit the specific conditions of a site, considering water and nutrient availability, pH values and available microhabitats. This would already cater for higher gamma diversity at regional level. *We included this point in Box 3 in the prior version and have now added it to the text.*

- L. 244: I think it is necessary at this point to specify the ethical and conservation aspects when collecting species from the wild. It may, moreover, be difficult to reproduce species ex-situ, which would, however, be necessary for re-introduction of species. I would appreciate consideration of this critical point, as restoration activities may also pose a negative impact on conservation activities in this case. *We have added a clause to note the importance of following best practices to minimize impacts of wild collection on source populations (lines 241-242), but feel that further discussion is outside the scope of this paper.*

- L. 274: This statement may be misinterpreted in a way that also non-native species can be entailed in restoration activities as long as a few rarely representation species from a regional pool are included. This however, strongly contradicts the earlier statement, that these species may outcompete the rarer and less competitive species that are often underrepresented. I suggest to revise this statement to avoid misinterpretation. Moreover, it would be good to specify which policies the authors are talking about in line 272ff and 275ff. Are these the same ones as referred to as "regulations" in line 278? *We have added "native" species to the noted sentence to address the point. We make general recommendations that could be included in different policies and regulations and offer a couple of examples to illustrate them, but don't think that more text is needed to match recommendations to specific policies given the many different relevant policies and legislation across the globe.*

- L. 302: The claim here is that authors have highlighted mechanisms and strategies to avoid biotic homogenization, but it is not clear from the text which mechanisms and strategies these are. I ask for a clarification of this for the reader. *We're not entirely clear why this sentence was confusing since the middle section of our paper was about causes of biotic homogenization and the last section is about recommendations to overcome the process. However, we have changed the wording to more closely follow our headers and have referred to Box 3.*

- L. 594: How should a practitioner know about these traits- maybe the authors could highlight a database for a specific case study area to encourage the use of this dimension of diversity in practise? *We provide some examples in the text and have added a link to the widely used TRY plant trait database as an example of where this information could be found.*

- L. 596: It could be helpful to link to an example of the guidelines. *We reference these guidelines in the text.*

- L. 600: Also here the expression of "widely accessible online formats" could be illustrative by providing an example. *We provide a reference in the text (lines 224-233).*

- L. 601: Add an example of such an exchange programme? *We reference one in Box 2.*

These four prior requests ask us to add citations in Box 3, which we have not done in this version, since we included references for each of these points in the text. We could add references in the Box but feel that if we were to do so, we should add references for each bullet point. If you would like us to do this please let us know.

Reviewer #3: OVERCOMING BIOTIC HOMOGENIZATION IN ECOLOGICAL RESTORATION

General comments: This article analyzes the dual role of restoration in promoting biotic homogenization and at the same time its potential to reduce it if certain measures are adopted to increase taxonomic, genetic and functional diversity. The idea of the article is new and potentially of interest to a wide range of readers. I agree that restoration, in practice, has contributed to the increase in biotic homogenization, however, I think it is important that the authors reflect on the level of demand that restoration has suffered. I am afraid that even pertinent criticisms of theory (such as the authors raise in this article) will be raised too soon for a relatively recent science. That said, I don't argue that one shouldn't anticipate major failures, but that we should carefully dose criticism. In a way, this is what the authors do when proposing ways to reverse biotic homogenization in restoration practices. Below, I present details on the points that I believe deserve special attention from the authors.

On the definition of biotic homogenization (BH) - The authors define BH in lines 15-16 of the manuscript imprecisely, in my opinion. BH is a process of increasing similarity between biological communities (reducing beta-diversity) over time. Therefore, in order to detect BH, it is necessary to observe the process over at least two periods of time. This is due to the fact that beta-diversity responds naturally to space and environmental filters, but in theory, not to time. One of the mechanisms that can result in BH is the replacement of specialized species for generalists ones. Therefore, there is a confusion between the process and the result of BH that needs to be clarified at the beginning of the article. Thus, I suggest that the authors rewrite the manuscript introduction mentioning that the definitive proof of BH is the reduction of beta-diversity over time and that this needs to be observed in restoration projects, too.

We agree that our definition of biotic homogenization in the introduction was too brief and not entirely consistent with the glossary. We have expanded it slightly to more clearly state that overcoming biotic homogenization requires increases in alpha and beta diversity. As discussed in responses to other reviewers, we have expanded our discussion of the temporal component of biotic homogenization later in the paper.

The evidence - In this section I suggest that the authors pay more attention to the theory and the question of time. For example, the evidence cited in Sapkota et al. that restored areas are more similar to each other than the reference forests is not surprising and speaks more of a process of environmental filtering or even of dispersal limitation (natural regeneration). It is not possible to say that it leads to BH unless comparisons were made between sites under natural regeneration and others under assisted regeneration (restored). Therefore, I think that the example used does not help the authors' line of argumentation.

The reviewer raises some interesting points here. The reviewer's comment suggests that he/she considers that natural regeneration/passive restoration is not a form of restoration. However, the Society for Ecological Restoration standards note[1] and we agree[2] that restoration interventions exist along a continuum which includes natural regeneration. Natural regeneration and assisted natural regeneration often include considerable cost and labor investments to facilitate recovery such as fencing land, controlling fires, grazing, and other disturbances, and compensation landowners for lost opportunity cost.

We think that comparisons of actively restored sites and reference forests are relevant to assess biotic homogenization in restoration, but also agree that it is valuable to compare beta- and gamma-diversity across multiple sites that were restored either using natural regeneration or more active restoration such as planting. However, after thoroughly reviewing the literature again we only found one study that compared beta- or gamma-diversity across multiple sites restored using different methods (e.g. many natural regeneration sites and many active planting sites), as well as reference sites. We have added reference to a citation Hayward, et al. [3] that compares beta- diversity across both naturally-regenerated and actively restored logged sites in dipterocarp forests in Borneo (lines 60-62). We have expanded one of our outstanding questions to address this gap in the literature.

Another important point is functional homogenization, which can be even more sensitive to human interventions than taxonomic. Again, comparisons between restored forests and reference areas allow, at most, to suggest BH but are not unequivocal evidence of this process. Functional traits may or may not be phylogenetically clustered; environmental filtering can therefore lead to both dispersal and phylogenetic clustering.

We agree with this point. We discuss both functional and phylogenetic homogenization in the "evidence" section noting that they are often (but not always) related. We could expand the text more here, but given that this was a somewhat tangential point, we decided to use our limited words to address other, higher priority comments.

I emphasize that comparisons between restored sites and reference areas do not seem to me to be strong evidence. Comparison between naturally restored and regenerated areas can be a much better indicator. Por favor, veja o artigo de Lobo et al (2011) (https://onlinelibrary.wiley.com/doi/full/10.1111/j.1472-4642.2010.00739.x) e note que os autores associam a perturbação da Mata Atlênica Brasileira como BH ao longo do tempo.

We reviewed the Lobo et al. (2011) paper which compares biotic homogenization in forest fragments in the Brazilian Atlantic forest and now cite it as an example of biotic homogenization in fragmented landscapes, but it does not provide a comparison between restored and reference sites. As noted above, we have done an extensive search for articles that compare regional diversity across naturally-regenerated and actively restored sites and have now cited the one relevant study we found. It is certainly a promising area for research and, in fact, one of us (Holl) is evaluating this question across multiple long-term tropical forest restoration sites in Costa Rica. But, we do not have any published results to date.

Causes of Biotic Homogenization in Restoration

Local and landscape context - In this section the explanations are much more useful for the authors' arguments. I agree that the proliferation of winner species tends to increase BH and this has already been evidenced in different works. Recently an article published in TREE by Filgueiras et al. 2021 (https://www.sciencedirect.com/science/article/pii/S0169534721000562) summarizes how landscape changes can lead to proliferation of "winner" species and disappearance of rare "loser" species. So, I would like to suggest for this session that authors discuss how restoration in fragmented landscapes can lead to BH or how they can increase beta-diversity. I can quickly imagine both scenarios. BH can be promoted by restoring disturbed landscapes if the increased availability of habitat and connectivity initially favors the "winner" species of the landscape. In fact, the issue of reconversion of secondary forests and the very "secondarization" of mature forests tends to reduce heterogeneity and promote BH. Which is more likely? Why? Under what conditions?

We do cite the Filgueiras et al. 2021 article and have condensed the points that overlap with this article. This section is only two short paragraphs as we recognize these points have been discussed elsewhere and just need to be summarized. In response to a comment by reviewer 1 and this comment we have noted that connectivity is less important in ecosystems that do not have high quality remnant habitats. We noted the issue of the secondarization of reference forest in the prior version (lines 120-123) and have added the Lobo et al. 2011 citation in support of this point.

Restoration actions and Recommendations to Improve Gamma-diversity - These sections are where I think the reviews get very demanding. The authors recognize the limits and practical reasons for the most widespread methods of restoration. I consider it important to point out that restoration agendas have matured and have incorporated more and more complex objectives over time, including the provision of ecosystem services. As far as the authors are aware, there is a trade-off between the ecological effectiveness of restoration and its political and economic viability. A large part of the restoration is taking place and will take place in working landscapes and therefore must serve different goals, including economic, social, cultural and biological.

I agree that the recommendations made to improve the practice of restoration and prevent this activity from promoting BH are important and should be pursued. However, given a realistic scenario, at least in theory, could we accept an increase in BH, even if momentary? Should we demand that restored areas play a relevant role in reducing BH?

Corollary - I believe that the topic discussed is important and very relevant for restoration, but I believe that it is possible that the authors can make a more relevant and stimulating theoretical contribution. There is great discussion about the occupation model of working landscapes, whether via land-sparing or land-sharing. How would restoration contribute to reducing or increasing BH in each of these scenarios? How can biocultural restoration, which is based on cultural values of the species, utilitarian or not, promote or reduce BH? Even in the worst case scenario, can a restored landscape that has suffered BH be managed to prevent this process from perpetuating itself? I believe that these are questions of great relevance to assessing the role of restoration in maintaining beta-diversity.

We strongly agree with the reviewer that we are asking a lot of restoration and that as the scale of restoration grows, particularly with limited funding, there will necessarily be tradeoffs between meeting biodiversity, carbon, human livelihoods and cultural values, and other goals of restoration. We had noted this in multiple places in the text (e.g. lines 32-35, 130-131, 165-168) and in the outstanding questions in our original manuscript. Nonetheless, we agree that it warrants further discussion and have expanded the text on the topic (lines 50-51,182-184, 299-310). In the conclusions, we note that there may be both tradeoffs and synergies between maximizing regional diversity and achieving other restoration goals, and provide an example where ecological, economic, and cultural goals have been achieved. A great deal has been discussed about the land-sharing vs. land-sparing debate and we feel that a detailed discussion of it is outside the scope of this article.

Minor comments

I guess the use of gamma-diversity can be replaced for beta-diversity. Gamma is a function of beta and mean alpha diversity (Wittaker). Gamma can therefore be improved both through high alpha diversity or community dissimilarity. Because the paper deals with BH, I suggest adopting Beta.

We understand reviewers' point, and prior to the first submission we had a lengthy discussion amongst ourselves and with others who we asked to review our paper about whether to focus on gamma or beta diversity. We chose to focus on gamma diversity, while at the same time recognizing the importance of increasing the beta-diversity component of gamma-diversity, for a few reasons. Our primary goal in this paper is to recommend how to improve regional biodiversity (gamma-diversity) which is a product of both alpha- (within site) and beta- (turnover across sites), which we now note more clearly in the introduction. As Socolar et al.[4] state thoughtfully, "Maximizing beta-

diversity is not necessarily desirable for gamma-diversity conservation, because damaging anthropogenic impacts can cause the similarity of local communities to increase, decrease, or remain unchanged, depending on the relative balance of homogenization and heterogenization processes at the site level ….Even when beta-diversity decreases, compensatory changes in alpha-diversity can buffer gamma-diversity against declines in beta-diversity."

A second reason for using gamma-diversity is that studies of beta-diversity range from very small-scale studies (e.g. beta-diversity on the order of meters to tens of meters) to the much larger scales that we are addressing here. Gamma diversity is largely used to address diversity at the regional scale, which is our focus. A final reason for focusing on gamma-diversity is that in conversations with practitioners, we have found that gamma diversity is an easier concept to understand than beta-diversity and its multiple components (e.g. turnover, nestedness), and we want to make this paper as accessible as possible to both academic and practitioner audiences.

I missed a more conceptual figure as Figure 1 is more like an example of the process rather than a framework. TREE journal is the perfect venue for stimulating new frameworks. Please try it!

We politely disagree with this reviewer that we should add another "more conceptual" figure without any specifics of what this figure might look like. We carefully designed the figure to illustrate several conceptual points of how restoration could increase (panel C) or decrease (D) biotic homogenization depending on how it is done. We refer to these points throughout the paper and in the caption. We spent many hours discussing and making several rounds of edits on our current figure, based on our discussions and feedback from colleagues, to ensure that it was as clear as possible and that it complemented the other Tables and Boxes in the paper. At this point, it is hard for us to envision an additional conceptual figure that would fit with the way we have written the paper, so it would essentially mean going back to square 1 on the paper. Moreover, neither of the other two reviewers commented on the figure, suggesting that they felt it was effective in communicating a number of our ideas. We plan to make a Figure 360 video to fully explain the various conceptual ideas illustrated in the figure.

References Cited

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3. Hayward, R.M. et al. (2021) Three decades of post-logging tree community recovery in naturally regenerating and actively restored dipterocarp forest in Borneo. *For. Ecol. Manag.* 488, 119036.
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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.

OVERCOMING BIOTIC HOMOGENIZATION IN ECOLOGICAL RESTORATION

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Keywords: gamma-diversity, diversity conservation, habitat heterogeneity, reintroduction, rewilding

Abstract

Extensive evidence shows that regional (gamma) diversity is often lower across restored than 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 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.

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, 2-4]. 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], 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 U.N. 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 to 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 to 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.

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 U.S. improved phylogenetic diversity, but not to the level in reference systems.

Likewise, a growing body of evidence suggests that restoration 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 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 to 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 a 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, 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 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 to 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 (Box 3). We acknowledge that many of these practices will increase the costs of restoration, and as such, will require careful consideration of tradeoffs 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 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 3, 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 3). 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 re-introduce 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 2). Projects that include restoration of rarer species and habitats could be prioritized for funding from public sources, such as the U.S. 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 U.N. 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 U.S. 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 U.N. 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 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 2), 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 3). 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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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. (2018) 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 [93] further addressed this question by measuring vegetation composition and conducting land manager surveys of 37 restored coastal prairies. The sites ranged in age from 3-30 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 species, 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.

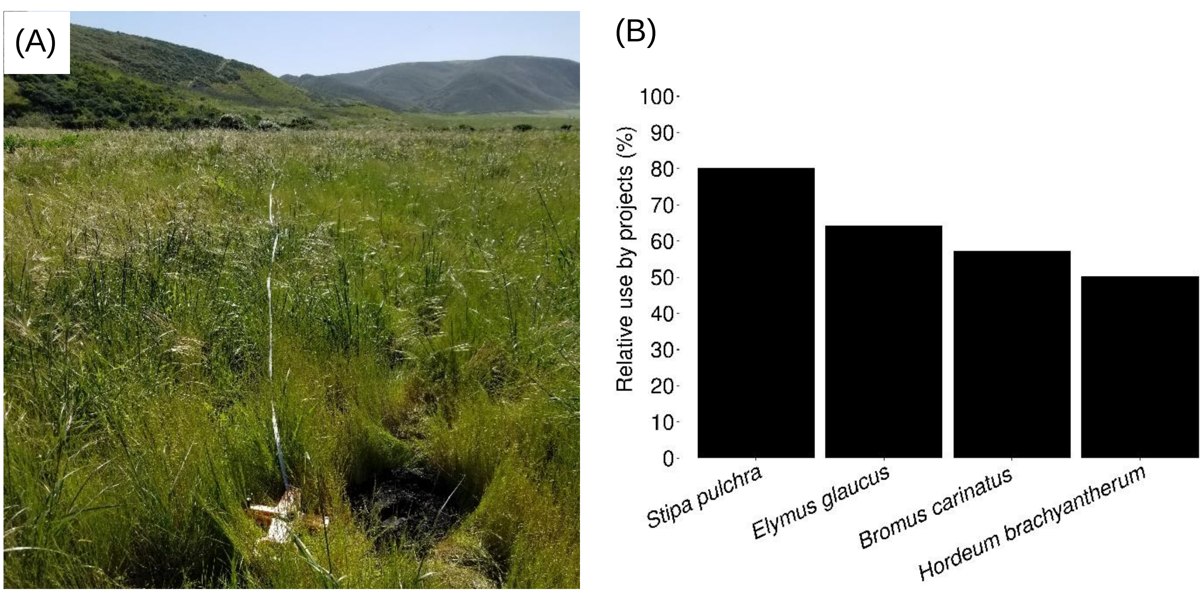


Figure I. (A) Restored coastal prairie dominated by one perennial grass, *Stipa pulchra*, a species that is commonly planted along the entire California coast. (B) Percentage of projects in which the most commonly used species were planted; practitioners preferentially selected these species because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

Box 2. 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 3,263 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, 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 underrepresentation 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 [94]; (ii) legal policies now require a minimum number of native tree species in restoration programs [95], (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 [96], which may promote the arrival of rare and threatened species in restoration sites.

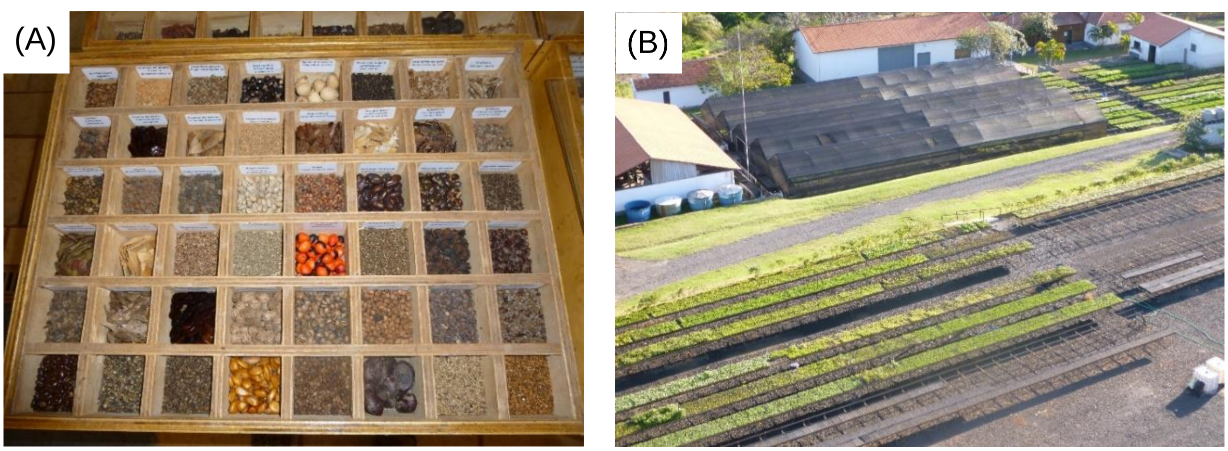


Figure II. (A) Collection of various Atlantic forest tree seeds used for restoration. (B) Large nursery with the capacity to produce ~1 million seedlings annually of a diversity of native species.

Box 3. 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
- Reestablish 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

GLOSSARY

Alpha-diversity: the species diversity of a relatively small area. For the purposes of this review, 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.

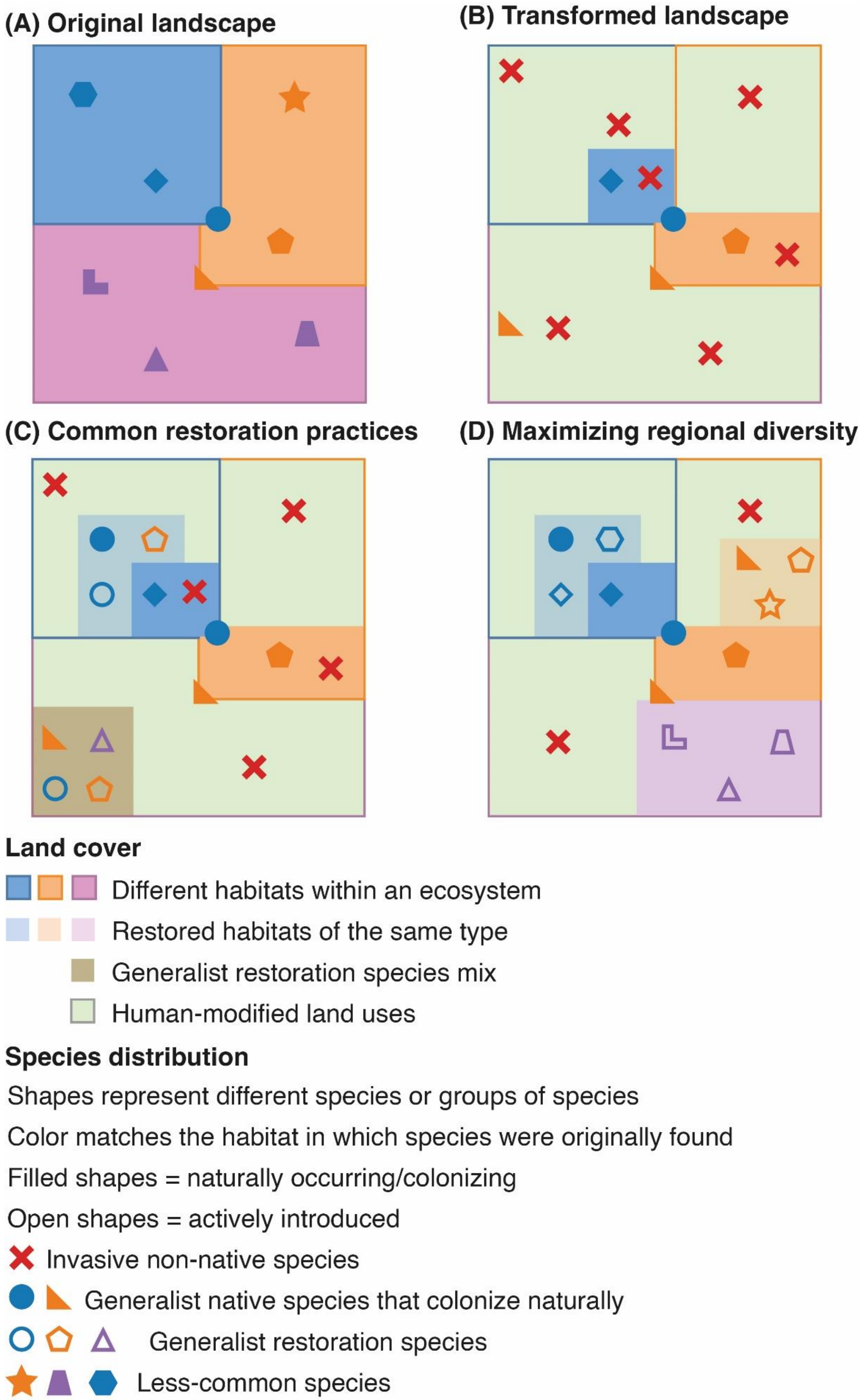
Habitat: variations of an ecosystem along abiotic gradients that support different species compositions. For example, California grassland composition differs as a function of soil type (e.g., serpentine grasslands) and soil moisture (e.g., wet meadows).

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

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

Type of homogenization	Examples	Citations
Lack of rare, specialized or endangered species	Temperate forest and grassland plants, grassland moths, wetland algae	[22-24, 97]
Low gamma-diversity across restoration sites	Grassland bees and plants, multiple tropical forests taxa	[2, 21, 24, 25](Box 1)
Predominance of certain functional traits	Peatland plants, tropical forests 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, 98]

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



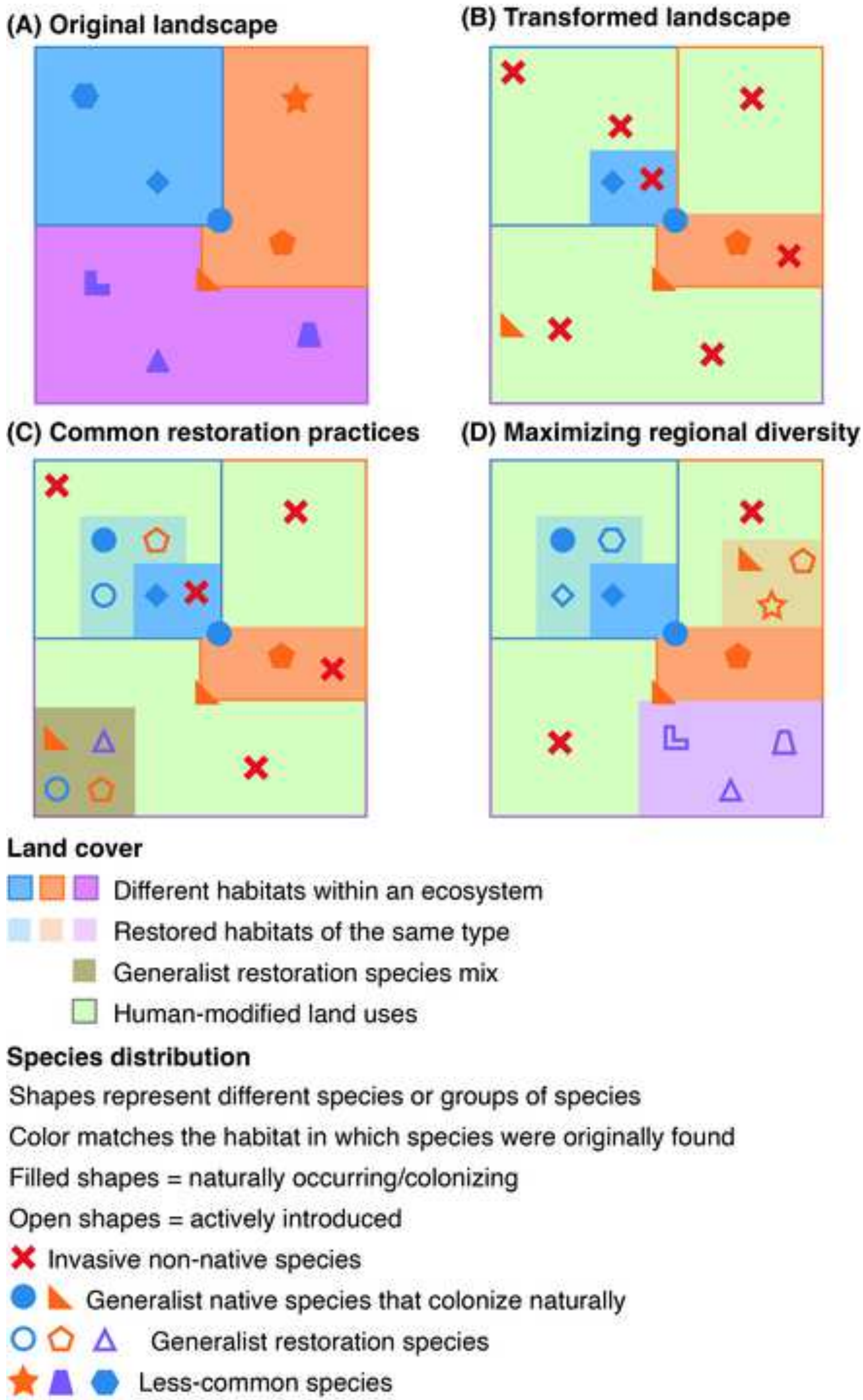
(A) Original landscape
(B) Transformed landscape
(C) Common restoration practices
(D) Maximizing regional diversity
Land cover
Different habitats within an ecosystem
Restored habitats of the same type
Generalist restoration species mix
Human-modified land uses
Species distribution
Shapes represent different species or groups of species
Color matches the habitat in which species were originally found
Filled shapes = naturally occurring/colonizing
Open shapes = actively introduced
Invasive non-native species
Generalist native species that colonize naturally
Generalist restoration species
Less-common species

Figure 1. Counteracting biotic homogenization of plants in restored landscapes. (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 more extensive efforts to control invasive species in restored habitat.

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?

Figure 1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Box 1 - Figure Ia

Box 1 - Figure Ib

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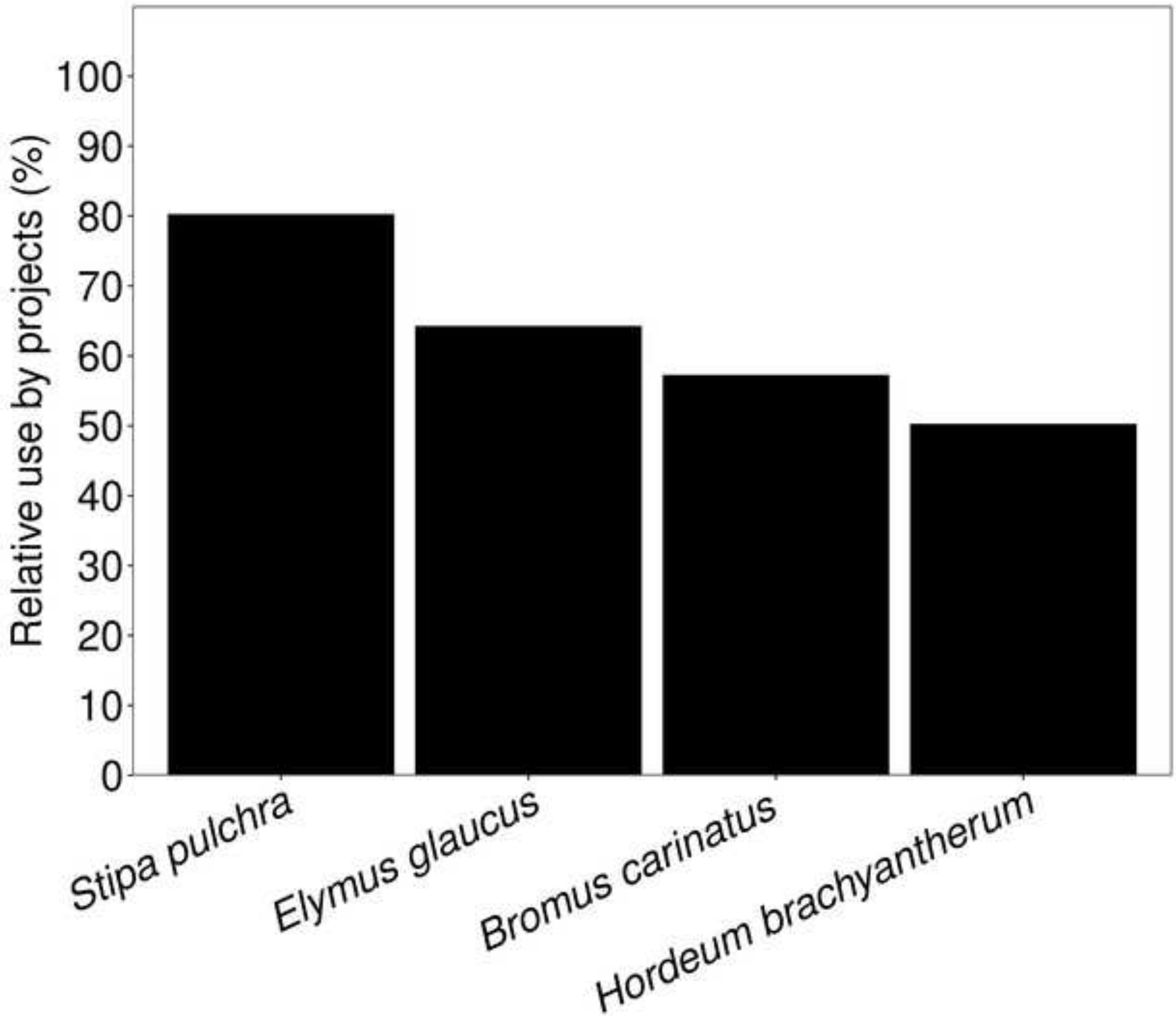

Box 2 - Figure IIa

Box 2 - Figure IIb

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