Harnessing Ecological Theory to Enhance Ecosystem Restoration

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Abstract: Ecosystem restoration can increase the health and resilience of nature and humanity. As a result, the international community is championing habitat restoration as a primary solution to address the dual climate and biodiversity crises. Yet most ecosystem restoration efforts to date have underperformed, failed, or have been burdened by high costs that prevent upscaling. To become a primary, scalable conservation strategy, restoration efficiency and success must increase dramatically. Here, we outline how integrating ten foundational ecological theories that have not previously received much attention – from hierarchical facilitation to macroecology – into ecosystem restoration planning and management can markedly enhance restoration success. We propose a simple, systematic approach to determining which theories best align with restoration goals and are most likely to bolster their success. Armed with a century of advances in ecological theory, restoration practitioners will be better positioned to more cost-efficiently and effectively rebuild the world's ecosystems and support the resilience of our natural resources.

Introduction

Recognition of the nearly indiscriminate, human-caused degradation of natural ecosystems and their life-sustaining benefits has catalyzed a century of conservation biology and practice[1]. Yet, after over 100 years of conservation in action, the primary interventions used by managers and governments (e.g., establishing protected areas, reducing pollution, regulating hunting and fishing, and limiting development) have mostly slowed and rarely reversed overall global trends in ecosystem decline[2–4]. While many of these interventions have been effective in certain situations (e.g., well-managed protected areas can reverse the decline of forests and endangered species, and effective fisheries management can guard against overharvest), these successes have not been enough. Consequently, the international community has recently advocated for the elevation of ecosystem restoration as a primary conservation intervention to help overturn continuing global ecosystem decline. In fact, the United Nations has called upon ecosystem restoration – defined as "the process of halting and reversing degradation, resulting in improved ecosystem services and recovered biodiversity"–, to act as a key strategy to help meet sustainability and climate adaptation goals for the globe[5]. The magnitude and urgency of this task were further emphasized by the UN declaring 2021-2030 the Decade on Ecosystem Restoration, kickstarted by setting the ambitious goal of restoring a globally-combined area the size of China by 2030.

To simultaneously meet the new demands of the international community and ultimately revitalize Earth's degraded ecosystems, restoration practice requires both an increase in spatial coverage and several strategic, practical shifts to rapidly increase cost-efficiency, scalability, and success. To address substantiated criticisms (i.e., restoration being a relatively expensive conservation intervention, typically small in scale, and failure-prone[6]), we propose key advances that can be implemented relatively quickly through a more systematic incorporation of fundamental ecological theory into restoration practices.

Ecosystem restoration has been presented as an "acid test" for ecology[7], and restoration ecologists have been advocating for practices to be grounded in natural history and ecological theory for decades[8–11]. For example, restoration of degraded plant communities has long been bolstered by successional theory and community assembly theory-based predictions on the progression and trajectory of restored communities[9, 145-147] and by innovations in seed-mix design informed by coexistence theory[148,149]. The application of other individual ecological theories has greatly improved restoration scale and success. Clear examples are facilitation theory in aquatic restoration[12], alternate stable state theory in herbaceous plant restoration[13], and landscape ecology theory for animal-based habitat restoration[14]. Yet, meta-analysis shows that succession theory and community assembly theory continue to dominate in those limited circumstances where restoration practices have incorporated theory[15].

Theoretical ecology has been unable to comprehensively change restoration practices, as most restoration studies use site- or species-specific information to inform design even as the mention of theory in restoration literature grows[15]. For example, fencing off plant restorations to protect outplants and seedlings from herbivores is a commonly used method that increases restored plant abundance by 89% and eclipses the effects of managing for plant competition or physical factors[16]. Yet, even though food web theory and empirical tests of that theory indicate that predators have wide-reaching, strong indirect effects on plants, relatively few restoration studies across global vegetated ecosystems consider predators in their design[16]. Likewise, over 100 peer-reviewed papers have called for the integration of positive species interaction theory into coastal ecosystem restorations because facilitation-informed restoration outplant designs can increase success by 100-300% in marshes and seagrasses[18,19]. However, less than 3% of over 600 salt marsh, seagrass, and oyster restoration studies incorporated positive species interaction theory[17]. So, why are current restoration practices not incorporating ecological theory more often? One key barrier may be a lack of direct guidance for *how* and *when* restoration practitioners should incorporate different theory-based strategies into their designs.

Here, we address this barrier by briefly summarizing a representative list of 10 key ecological theories that our team of interdisciplinary ecologists and restoration practitioners have identified as essential but underutilized in restoration. To aid restoration managers in the systematic integration of ecological theories into ecosystem restoration designs, we present a flow chart outlining a start-to-finish approach for planning, implementation, and assessment of theory-supported restoration (Figure 1). Instead of focusing on the reference state, the restoration approach to harness theory begins with the selection of a target ecosystem and/or species (Step 1) and the setting of restoration goals are set (Step 2). These goals are then prioritized based on stakeholder input (Step 3) and grouped by biological level of organization (Step 4). To integrate restoration and theory we provide a reference table (Table 1) that guides practitioners to theories that then apply most appropriately to their conservation goals (Step 5). We then outline these essential but underutilized theories and present possible restoration applications based on specific management and conservation goals. Overall, we seek to both empower restoration managers with digestible and applicable ecological theory and to urge academically oriented ecologists who work directly with practitioners towards these underused theories to lower knowledge barriers by providing a common understanding and conceptual framework.

Competition Theory: Manipulating both the strength of competition (i.e., the process through which species vie for limited resources) and the likelihood of priority effects (i.e., when competitive outcomes depend on the timing of arrivals)[22] can be a key strategy to bypass competitive hierarchies that would otherwise suppress establishment restoration-targeted basal species, such as trees or corals. Competition influences how communities form and function in all ecosystems and managing key competitive species interactions, like removing invasive or native competitors, has proven critical for promoting targeted species establishment. For example, by removing invasive grasses from wetland prairie seedbanks prior to restoration, managers can reduce the strength of competition for space and increase outplant growth rates and native plant diversity [21].

While managing for invasion or competition to aid in restoration community assembly is becoming more common[15], similarly wide-reaching priority effects have a more cryptic and often unconsidered influence on community establishment. Priority effects related to the identity, order, and timing of species' arrival often dictate the competitive outcomes that drive community assembly[20]. Thus, management to prevent early-arriving species from depleting resources and to deter invaders with similar niches (i.e., niche preemption [23] or niche modification)[20,24–26] can boost establishment success. The strength and persistence of priority effects depend on the biotic and abiotic context [27], and managers can manipulate this context to bolster restorations. For example, planting a competitively-inferior target species in aggregated patterns of conspecifics can generate “spatial priority effects” [28], that increase focal species’ growth before coming into contact with stronger competitors. Temporal priority can also be maintained through scheduled seeding or planting times to directly control the timing of both community assembly and the manifestation of ecosystem functioning [29]. Communication and collaboration between practitioner and experimental ecologist partners will be essential to determine competitive hierarchies and the outcome of priority effects, as life history knowledge and reciprocal transplant studies may be necessary to elucidate mechanisms that might release focal species from competitive pressure.

Figure 1. Harnessing Theory Decision Flow Chart. Suggested steps for practitioners and ecologists to implement a restoration project together that is fully integrated with ecological theory. See Figure 7 for a worked example.

Table 1: Information needed to complete step 5 in the decision flow chart (Figure 1). Biological level of organization of desired outcomes (step 4) linked to related ecological theories (step 5) with associated reference material.

Biological Level of Restoration Outcome:	Related Theories:	References:
Genes	Evolution (e.g. selection, drift)	Rice et al., 2003, Futuyma & Kirkpatrick 2022
	Metacommunity Theory (i.e. Dispersal)	McKay et al., 2005, Leibold 2018
	Competition Theory (intra)	Hartl & Clark 2007
Organism	Facilitation Theory	Camazine et al., 2003
	Metabolic Theory	Brown et al., 2004, Sibly et al., 2012
	Self Organization Theory	McCann 2012
	Ecological Trap Theory	Hale & Swearer 2017
Population	Metapopulation Theory	Maschinski & Quintana-Ascencio 2016
	Metabolic Theory	Brown et al., 2004, Savage et al., 2004
	Self Organization Theory	Zhao et al., 2019
	Facilitation Theory	Silliman et al., 2015
	r/K Selection Theory	MacArthur & Wilson 2001, Reznick et al., 2002
	Ecological Trap Theory	Hale & Swearer 2017
Community	Food Web Theory	Zanden et al., 2016, McCann 2012
	Facilitation Theory	Gómez-Aparicio et al., 2004
	Metacommunity Theory	Leibold et al., 2004, Holyoak et al., 2005
	Neutral Theory	Hubbell 2001
	Hierarchical Organization Through Facilitation Cascades	Palik et al., 2000
	Resilience and Disturbance Theory	Gunderson 2000
	Metabolic Theory	Brown et al., 2004
	Self Organization Theory	Solé & Bascompte 2006
	Coexistence Theory	Chesson 2000
	Mesopredator Release Theory	Estes et al., 2013
	Competition Theory (inter)	Bolnick et al., 2011
	Community Assembly Theory	Fukami 2015
Ecosystem- Function	Facilitation Theory	Gómez-Aparicio et al., 2004
	Metabolic Theory	Brown et al., 2004, Schramski et al., 2015
	Biodiversity - Ecosystem Function (BEF)	Loreau et al., 2003, Montoya et al., 2012
	Mesopredator Release	Ritchie & Johnson 2009
Ecosystem- Service	Metabolic Theory	Brown et al., 2004, Schramski et al., 2015
	BEF	Loreau et al., 2003, Montoya et al., 2012
	Ecological Systems Theory	Levin 1998
Ecosystem- Resilience	Hierarchical Organization Through Facilitation Cascades	Palik et al., 2000
	Resilience and Disturbance Theory	Gunderson 2000
	Metacommunity Theory	Leibold et al., 2004, Holyoak et al., 2005
	BEF (i.e. Biodiversity-Stability)	Loreau et al., 2003, Montoya et al., 2012
	Spatial Patterning Through Self Orginazation Theory	Solé & Bascompte 2006, de Paoli et al. 2017

Food Web Theory: Because the connectivity, diversity, and evenness of local producers, consumers, and predators (i.e., food web structure) control wide-reaching processes in all ecosystems, incorporating food web theory into restoration will increase early success and stability in many habitats. All ecosystems have food webs, and the structure of these food webs have predictable bottom-up and top-down consequences for ecosystems. From the bottom-up, changes to the identity, diversity, and abundance of primary producers at the base of food webs control the density, diversity, connectivity, and/or trophic position of all other organisms in the ecosystem [30,31]. In addition, both the number of trophic levels in a food web and overall biodiversity are positively affected by the continuous spatial extent of foundation species [32,33]. From the top down, one of the oldest ecological theories posits that the globe is “green” – i.e., that plants are the most abundant organisms by biomass – because predators keep herbivores in check [34,see also 35]. Decades of experiments across systems and taxa [36] have shown how both consumptive and non-consumptive predator effects control the diversity and abundance of primary producers, foundation species, and keystone species that enhance ecosystem functions and services [37–39].

Progress in food web theory has led to general predictions about trophic control in ecosystems that we argue should be part of the restoration manager repertoire: 1) the number of trophic levels predicts plant success at the bottom of the food web – odd-numbered, trophic levels facilitate plants[40,41]; 2) ecosystem spatial extent (i.e., size) increases the number of trophic levels in aquatic ecosystems[42], whereas primary productivity does so in terrestrial systems [43]; 3) grazer control of plant diversity grows stronger along increasing plant productivity gradients [16,44]; 4) more complex food web structure (e.g., high connectivity, number of trophic levels, within guild diversity) may enhance ecosystem resilience to invasion and disturbance [45,46]; and 5) intraspecific diversity (e.g., genetic diversity or phenotypic diversity) can influence species connectivity and trophic level [47].

Food web theory can be included in the planning stages of all restoration endeavors systematically. By managing patch size of restored foundation species (i.e., ecosystem spatial extent), managers can maximize diversity provisioning and build new patches when diminishing marginal returns kick in. In ecosystems with clearly defined trophic levels, restoration sites can also be chosen based on food web structure, where odd-numbered trophic levels should be sought out for natural trophic control and overabundant herbivore sites could be strategically avoided. By managing predator presence or reintroducing locally extinct predators for enhanced herbivore control at the onset of ecosystem regrowth, primary producer restoration recovery or growth rates will improve. For example, reintroducing native predators increases the growth of outplanted terrestrial plants by ~370% on average[16]. However, social barriers may need to be addressed before using top-down control to aid in restoration, as predator reintroductions often require public information campaigns to gain acceptance. In the meantime, managers may need to creatively and manually implement herbivore control by mimicking predator presence through herbivore exclusions and promoting non-consumptive effects (e.g., shark mimics to deter corallivorous reef fish) in areas where predator reintroduction is undesirable.

Facilitation Theory: Facilitation theory-informed restoration can amplify beneficial interactions to improve establishment success and stability in stressful and high-disturbance habitats, a common ecosystem state for restorations. Positive interactions like facilitation or facultative and obligate mutualisms are pervasive in stressful habitats like alpine and prairie grasslands [48–50], the rocky intertidal [51,52] and salt marshes [53,54]. Indeed, the stress gradient hypothesis [55] predicts that stress amelioration by intra- or inter-specific neighbors is more common and more important in physically and biologically harsh habitats. Additionally, associational defenses among species are more common and important in habitats with high consumer pressure. The success of primary and secondary pioneer species in stressful habitats depends on either facilitators (e.g., microbes or habitat ameliorating neighbors) or on consumers (e.g., apex predator consumer control; see Food Web Theory) [12,56,57]. For example, networks of fungal mycelia distribute limiting resources among trees in old-growth forests [58](Figure 2a), a powerful mussel and marsh plant mutualism ameliorates physical and biotic stress to increase carbon sequestration, nursery habitat, and biodiversity in salt marshes[18,59,60](Figure 2b), and algal symbionts and coral neighbors underpin ecosystem development and persistence in coral reefs [61–63](Figure 2c). Yet, forests, salt marshes and coral reefs have historically been managed and restored only considering physical conditions and competition.

Positive species interactions that currently fuel productive but stressed ecosystems may increase the likelihood of restoration success in bare, degraded, or destroyed habitats [18]. In salt marsh restoration, promoting intraspecific facilitation between marsh plants (i.e., clumping outplants instead of dispersing plantings) mitigates sediment hyper salinity and anoxia to triple outplant growth and survivorship [18]. Likewise, by leveraging interspecific effects of clam fertilization on seagrass seedlings, adding clams to seed-based seagrass restoration increases propagule growth by ~200% [64]. In restoration of denuded, semiarid plant communities, inoculation of arbuscular mycorrhizal fungi and nitrogen-fixing bacteria enhances key species establishment and ecosystem functions[150]. Actively using specific, yield-boosting plant-microbial symbionts in terrestrial and coastal restoration holds merit but is still in its infancy despite agricultural practices relying on this technique for decades[151]. Because positive interactions are essential for the emergence and persistence of most ecosystems, systematic incorporation of facilitation across spatiotemporal scales is crucial for attaining stable, resilient, and self-sustaining rebuilt ecosystems.

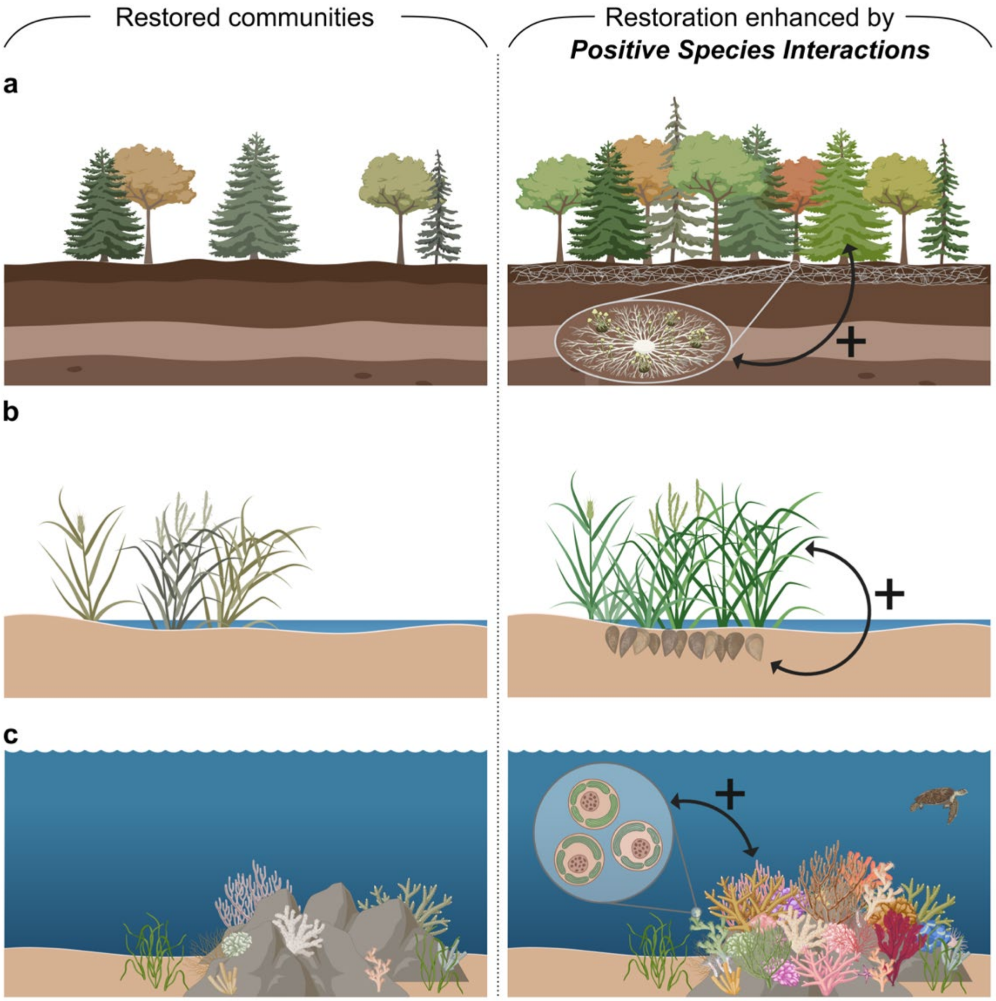

Figure 2. Using *Facilitation Theory* to enhance restoration through positive species interactions in different ecosystems. (a) Mutualisms between trees and fungal networks that distribute limiting resources improve restoration in old-growth forests. (b) Mutualisms between mussels and marsh plants reduce physical and biotic stress to enhance restoration in salt marshes. (c) Mutualisms between algal symbionts and corals underpin ecosystem development in restored coral reefs.

Hierarchical Organization Through Facilitation Cascades: As an expansion of facilitation theory, the concept of hierarchical organization through facilitation cascades predicts greater gains in restoration of foundation species, and in related diversity and function, if secondary foundation species are incorporated into restoration plans. By combining facilitation, priority effects, and food web theory to predict patterns of biodiversity in harsh environments [65], this integrated approach posits that physically-tolerant primary foundation species (e.g., salt marsh cordgrass, trees) initiate a hierarchical community structure by ameliorating biotic and abiotic stress upon establishment, thereby setting the stage for establishment of other species and community interactions. By increasing biodiversity and spatial resource heterogeneity (see: Facilitation), they also have wider-reaching, larger-scale positive effects by creating the conditions that promote secondary foundation species establishment [e.g., 66]. This cascading facilitation creates more microhabitats, increased niche space, and higher resource heterogeneity that in turn drives substantially higher biodiversity and ecosystem function [67–69]. For example, on wave-stressed cobble beach shores, salt marsh plants (primary foundation species) provide physical and biotic refuge for mussels (secondary foundation species) that form extensive intertidal reefs under the protective marsh canopy. The complex marsh plant-mussel reef, overlaid on the cobble beach, then provides complex refuge and food for littoral organisms that would otherwise be excluded from these habitats by physical and biological stress [65]. Observations and experiments in mangroves, sand dunes, deserts, maritime forests, and forest ecosystems confirm the generality of this theory: hierarchical establishment and organization of foundation species promotes cascading positive interactions that regulate ecosystem productivity, biodiversity, and recovery from disturbance[70–74].

For restoration, the hierarchical organization model predicts that the probability of biodiversity goals being met by restoring secondary foundation species depends on: 1) the degree of functional and morphological similarity between primary and secondary foundation species, 2) the spatial configuration of the two foundation species, and 3) secondary foundation species abundance[66,71,74] (Figure 3). Thus, for restoration in stressful ecosystems, high functional trait divergence among hierarchically-organized foundation species (i.e., a complementary secondary foundation species, Figure 3a) is predicted to simultaneously maximize habitat availability, community abundance, and biodiversity[33,74].

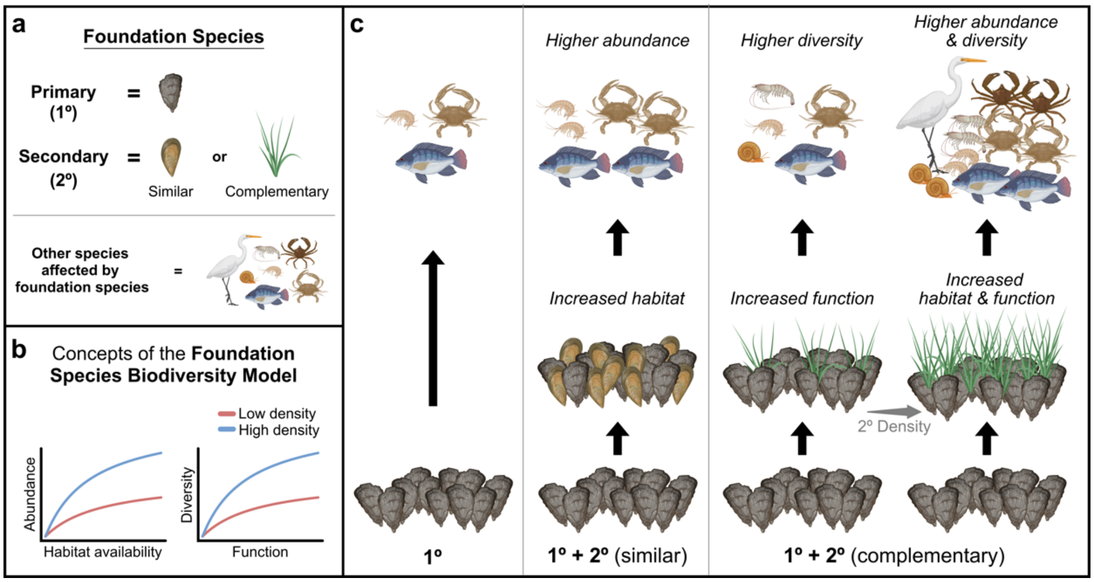

Figure 3. Using hierarchical organization theory to enhance restoration of biodiversity and ecosystem services. (a) The hierarchical organization through facilitation cascades model distinguishes between primary (1°) and secondary (2°) foundation species. (b) Key concepts of this model are that i) 2° species that increase habitat availability enhance species abundances and ii) 2° species that provide additional functions increase species diversity. Both effects are elevated at higher secondary foundation species densities. (c) Example of the Foundation Species Biodiversity Model in intertidal oyster reefs in the southeastern United States. Oysters are a common primary foundation species, while common secondary foundation species include mussels that provide *similar* structure and function and salt marsh grasses that provide *complementary* structure and function. While 2° species are predicted to increase either habitat availability or ecosystem functions, leading to higher abundance or diversity of inhabitants, respectively, high-density 2° species are predicted to increase both abundance and diversity of inhabitants. Adapted from [74].

Metacommunity Theory – For restoration of highly fragmented and/or naturally patchy habitats, metacommunity theory informs how dispersal dynamics will affect the initial establishment and long-term persistence of restored populations. Metacommunity theory explains trajectories of communities by incorporating both the dispersal limitation and spatial processes that control extinctions and re-colonization across local, regional, and global scales [75]. According to this theory, connections between local communities by dispersal can play a fundamental role in species population establishment and persistence [76], including the maintenance of within- and across-patch genetic diversity which may enhance resilience to disturbance or environmental fluctuations [77]. Restoration projects could incorporate metacommunity theory in their plans to simultaneously achieve recovery of populations that are resilient to disturbance and resistant to environmental changes across landscapes [78,79].

Landscape fragmentation threatens many natural habitats and restoration efforts by limiting between-patch dispersal and connectivity. Careful spatial planning incorporating metacommunity dynamics includes deciding the number, size, and spatial configuration of restoration patches to manage the overall connectivity among restored and remnant natural patches in the landscape [80,81]. On one hand, in cases where between-patch dispersal is strongly limited due to high fragmentation or inhospitable habitats between fragments, even if initial re-colonization is successfully achieved, connectivity can be enhanced by human intervention in the form of dispersal corridors among metacommunity patches (Figure 4). Importantly, corridors must be designed based on ecological theory by accounting for disperser behavior as well as establishing natural landscape features that mimic the conditions in the focal restoration patch[152]. On the other hand, high connectivity can be undesirable in cases where the target species are inferior competitors (e.g., they may be outcompeted by invasive species) or there are risks of disease/enemy spread [82]. In these cases, management may try to decrease connectivity, at least until the restored ecosystem has been established.

The potential positive outcome of incorporating metacommunity dynamics is highlighted by one of the most successful examples of in-practice application of this framework: the design of California's network of Marine Protected Areas (MPAs). During the design process, and to optimize both conservation and economic outcomes, the number of individual MPAs, their size, and their spacing were determined by models of ocean circulation, larval distance capacities, species spatial population dynamics and even fishing effort [83,84].

Non-Linear Disturbance Threshold Theory: For ecosystems with strong nonlinear dynamics, integrating nonlinear threshold dynamics can greatly improve restoration success and efficiency. Ecosystem dynamics long thought to change gradually and linearly with increasing disturbance frequency or strength are now recognized as nonlinear, with thresholds in the level of disturbance-resilience [85]. Ecosystems may change relatively little, or even increase in diversity or productivity under low or intermediate levels of disturbance [86,87]. But, once a threshold frequency or strength of disturbance is exceeded, sudden and abrupt changes can take place to push an ecosystem into an alternative stable state [88]. In some cases, the disturbance threshold for ecosystem collapse is similar to the threshold where it recovers. However, when the recovery threshold is at a lower disturbance level than the initial threshold of collapse, as is hypothesized for ecosystems that are maintained by facultative mutualisms [89,153], ecologists and managers are challenged to predict ecosystem dynamics under this "hysteresis" [90]. Nonlinear threshold models with and without hysteresis can describe restored ecosystem dynamics under disturbance.

Nonlinear threshold ecosystem dynamics have been reported in myriad ecosystems, such as lakes, grasslands, forests, salt marshes, and coral reefs [91] with anticipated collapses above certain thresholds of anthropogenic impacts (e.g., climate or land-use change). Demonstrating the existence of these thresholds in ecosystem responses to disturbances has been experimentally challenging, particularly at large scales. However, a variety of statistical methods are being developed to detect early warning signals for potential abrupt ecosystem shifts [92]. Despite acknowledging threshold ecosystem dynamics for decades, ecologists currently lack a predictive understanding of when and where ecosystem shifts are linear or nonlinear, with or without hysteresis. Physical and biological factors affect the thresholds beyond which ecosystems decline, recover, or show resilience to disturbance. Both intensifying human and/or climate press drivers (e.g., increasing mean nitrogen deposition or temperature) that slowly change conditions and pulse disturbance events (e.g., heavy rainfall events, heatwaves) can generate shifts between alternate stable states. Additionally, grazers can lower the tipping points of salt marshes and temperate forests to drought [93,94], overfishing can lower the tipping points of kelp forests to climate warming [95], and invasive species have been found to either lower or increase the tipping points of lake ecosystems [96].

For restorations, understanding potential thresholds can guide restoration design and implementation specifically to reduce human disturbance to levels below these thresholds. Ignoring such thresholds could result in failure due to insufficient disturbance reduction, or unnecessarily high costs to reduce disturbance. Second, recognizing potential thresholds can help in the management of ecological factors that modify these thresholds. Restoring sea otters, for example, has allowed degraded seagrasses to recover despite high eutrophication levels [97]. Also, restoring seagrasses beyond certain thresholds that enable positive feedbacks can boost restoration success [98].

Biogeography/Macroecology Theory – When designing large-scale restoration projects, accounting for macroecological patterns in species distributions and biological processes can help to avoid the pitfalls of a one-size-fits-all approach. Biogeographical patterns have been documented for centuries (e.g., Linnaeus (1735) and Georges Buffon (1761) recorded where species could be found across latitudes and longitudes[100]. Now, biogeographical approaches describe how organisms are distributed over space and time and which factors underpin these distributions [99,100]. Two post-hoc biogeography theory explanations for observed patterns are especially relevant to the success of restoration across large-spatial scales: the strength of species interactions and levels of nutrient availability both change with latitude. Predation and herbivory are suggested to be stronger in tropical regions than in temperate regions [101 but see 154], evidenced by increased rates of avian nest predation [101], leaf herbivory by insects in forests [102,103], attack rates on caterpillars by arthropods [104], and herbivory in salt marshes by grasshoppers and snails [105,106]. Similarly, temperate regions are more nutrient-limited than tropical regions [107], as nutrient additions in temperate sites create much greater increases in herbivory than in tropical sites.

These biogeographical theory predictions lead to expectations for restoration results over space and time. For example, in tropical areas, restoration of foundation species is more likely to be undermined by intense herbivory [16] or nutrient limitation than a similar restoration in a temperate zone. To mitigate this, restoration practitioners in tropical sites may consider incorporating grazer exclusions or nutrient enrichment into their designs that are not required for their temperate counterparts. For instance, excluding grazing cattle from a tropical dry forest restoration project in Mexico resulted in a 20-fold increase in moth and butterfly species compared to grazed sites [108]. Likewise, salt marsh restoration practices in temperate areas that are eutrophic are more likely to need grazer exclusions because the marsh grasses are relatively more susceptible to overgrazing when nitrogen availability increases[155].

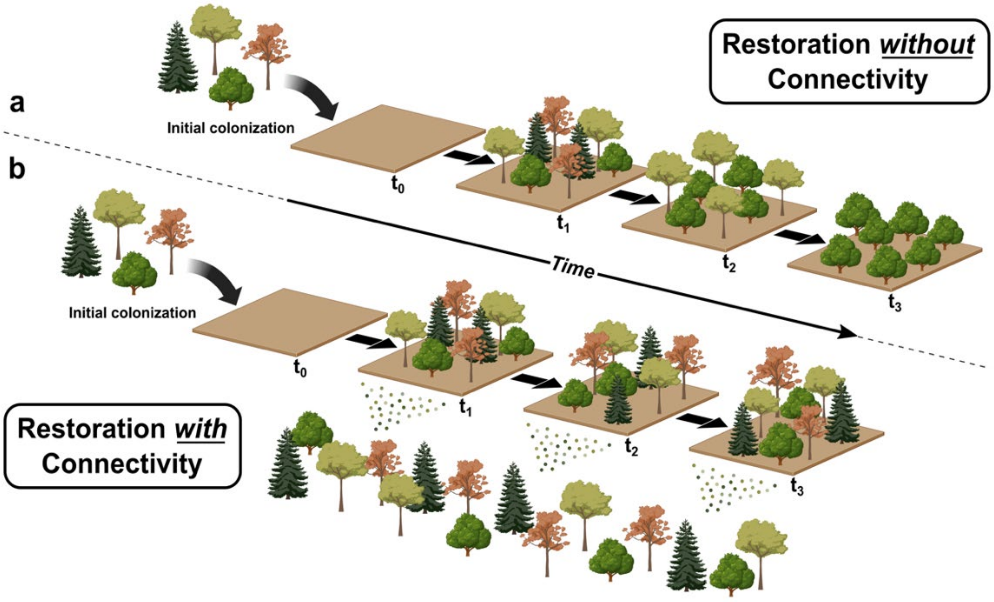

Figure 4. Effect of alternative connectivity strategies on biodiversity of restored sites over time. Forest restoration over time, from degraded bare ground (t_0) to restoration initialization (t_1), over medium (t_2) and long (t_3) time scales. (a) After colonization of a restoration patch, competition, consumption/disease, environmental fluctuations, and/or ecological drift drive loss of species over time, decreasing biodiversity.

(b) Species loss over time can be compensated by recolonization and mass effect if restoration patches are connected to pristine patches or other restoration patches through spatial planning or dispersal corridors-represented here by a flow of propagules (dots)- maintaining or increasing biodiversity.

Metabolic Theory. Metabolic theory can inform restoration of ecosystem services, especially under rising temperatures. Metabolism is the conversion of energy and materials by living systems to power the activities of life. Metabolic theories place metabolism as the core ecological process, complementing the central role of population dynamics in other ecological theories. Metabolic theories explain how the rates of many ecological processes are influenced by organism-level metabolic rates, which are highly sensitive to body size and temperature of the organism[109]. Metabolic scaling describes the predictable influence of body size and temperature, via their effects on metabolic rates, on ecological functioning from organism to ecosystem scales [109]. Such metabolic scaling can inform restoration of ecosystem services, especially under rising temperatures. Because metabolic rate constrains rates of activities in individuals, populations, communities and ecosystems [109–111], allometries between metabolism and body size can systematically be used to predict organismal function across systems and taxa: larger systems use energy more efficiently (i.e., the economy of scale)[112], while warmer systems use energy at higher rates, until they can no longer function [e.g., 113]. Metabolic theory has been employed to project changes in the distribution and productivity of fish [114,115] and forests [116–118] with climate change. It has also been used to consider how microbial interactions can be included in ecosystem monitoring [119] and to predict coordinated changes in microbial community structure, dynamics, and ecosystem functioning under warming [120]. Because of the fundamental nature and importance of the relationship between body size, temperature, and metabolism, as well as its predictive power, integrating Metabolic Theory into current restoration practices can enhance restoration success [121].

More specifically, metabolic theory makes several predictions and anchors several ecological processes and theories relevant to restoration efforts, including food web theory, competition theory, and biogeography. For instance, bigger animals occupying higher trophic levels, have a greater metabolic demand and have a larger diet breadth than smaller animals [122]. Restoring large-bodied animals successfully thus requires not just accounting for these increased metabolic needs, but also can be enhanced by using metabolic theory to predict the size of foraging area required for healthy populations. Thus, metabolic theory informs population/organismal-level restoration goals: if restoration goals are to enhance growth, focusing on small or medium individuals is recommended and if goals are to enhance individual output, large-bodied individuals should be the focus. Also, metabolic theory mechanistically links metabolic rates and, thus, energetic demands, to environmental temperature [123]. Thus, restorations in areas with significant anthropogenic temperature change – such as streams, forest fragments or urban landscapes experiencing local changes in thermal regimes - must account for increased metabolic rates and growth rates, earlier maturation, and reduced lifetime reproductive outputs [124]. With an increasing need to consider how restoration efforts will fare under global change scenarios, metabolic theory has the potential to be a uniquely powerful tool to account for possible shifts in body size distributions and increased energetic demands imposed on rebuilt ecosystem structure and function in a rapidly warming world[156].

Spatial Patterning through Self Organization - Models of spatial pattern formation suggest that post-disturbance recovery and restoration are faster if the spatial pattern remains intact and if new recruit spatial patterning mimics the original spatial pattern of the system. In many ecosystems that are considered for restoration, the original spatial structure (e.g., streams, patchiness, topography) has been lost, especially in cases where agricultural practices have homogenized the landscape. This loss of spatial structure may limit restoration efforts and make it difficult for species to gain a foothold. Naturally, ecosystems are complex entities, and ecosystem functioning is shaped by a plethora of interactions between species and their environment [125,126]. These interrelated processes can create coherent spatial patterning (e.g., biotic bands, mounds or patches) in ecosystems like arid bushlands, intertidal mussel beds, peatlands, and coral reefs [127]. These spatial patterns, in turn, determine ecosystem functioning and resistance to environmental change such as drought and storms.

The consequences of complex pattern formation may need to be accounted for in real-world restoration projects. For example, mussel restoration on wave-swept intertidal flats showed that a natural banded out-plant patterning, in contrast to random or equally-spaced patterning, increases both mussel survival and overall restoration success[129]. Relying on spatial patterns to enhance ecosystem restoration has long been used by traditional farmers in degraded arid lands. By intentionally placing stone or bush ridges called “water bunds” to create equally spaced contour lines that obstruct run-off pathways, farmers in Sub-Saharan Africa successfully increase the capture and storage of water and nutrients[128] (Figure 5). The efficiency of these spatially patterned ridges is vital for plant restoration and cultivation and could not be achieved without accounting for ecologically important spatial patterns in resource provisioning. Thus, to optimize restoration success, the spatial pattern of resource sinks (the area where resources such as water and nutrients accumulate) should mimic the natural spatial patterns originating from self-organized spatial pattern formation [128,130].

Figure 5. Examples of co-opting natural ecosystem self-organization for restoration. By intentionally placing bunds, stone or bush ridges, to create equally spaced contour lines that obstruct run-off pathways, farmers in Tanzania (top left), Burkina Faso (bottom left), Kenya (right), and more successfully increase the capture and storage of water and nutrients. Photo sources: Justdiggit (top left, right) and Natuurpunt (bottom left).

Biodiversity – Ecosystem Functioning Theory (BEF). Biodiversity-ecosystem function theory makes valuable predictions that may enhance restoration outcomes across a hierarchy of scales. The variety of life, across ecosystems and trophic levels, enhances ecological processes. Biodiversity-ecosystem functioning theory posits that the diversity of species, species traits, and/or genetics consistently increases the rate of ecosystem functions and their stability over time[157]. Additionally, higher within-organism trait or genetic diversity generally increases population survival and growth, while within-population trait or genetic diversity generally increases resistance and resilience to disturbance[158]. Biodiversity enhances broad ecosystem processes through either the stabilizing benefits associated with having multiple species that can perform similar roles (i.e., functional redundancy) or the benefits associated with having a suite of species that perform different roles (i.e., functional complementarity). Both mechanisms for biodiversity to enhance ecosystem functions can also enhance restoration outcomes.

First, at individual restoration sites, trait diversity (e.g., different sized trees outplanted for restoration) will promote niche complementarity, facilitation and trophic feedbacks[131,132]. Furthermore, trait diversity provides the raw material for ecological selection and leads to dominance of high-performing genotypes or species (Figure 6a). Indeed, especially at small spatiotemporal scales (i.e., at an individual restoration site), genotypes or species with specific traits can maximize functioning or resilience[159]. Next, across restoration sites in a region, increasing species and/or trait diversity creates niche differences within communities and/or populations[160] (Figure 6b). Combined with adequate dispersal, species will dominate where they are best-suited to maximize restoration success across land- and seascapes[160] (Figure 6b). Biodiversity also provides temporal insurance: species' differences in environmental responses (i.e., response diversity) lead to asynchronous dynamics that protect restoration projects from climatic extremes[161] (Figure 6b). With climate-induced range shifts, managers may revisit the changing regional biodiversity pool to bolster response diversity (Figure 6c). Although emerging evidence supports spatiotemporal insurance effects in real communities[162], these mechanisms can be disrupted by certain competitive interactions, stochastic processes, or extreme levels of connectivity and dispersal.

Theory and evidence indicate that biodiversity provides an indispensable asset to planners as restoration programs expand in scale and face accelerating climate change [see 133, 163]. Given information on species' traits and natural history knowledge, managers may be able to tailor species composition to best capitalize on known mechanisms of complementarity or spatial insurance. Yet, uncertain species' responses to multiple and novel emerging stressors means that embracing biodiversity is a prudent risk-reducing, bet-hedging strategy. Nevertheless, managers could potentially boost the positive effects of biodiversity on species survival and ecosystem functioning in restored communities by including more well-adapted or high-functioning species, thus reducing the risk of failure (Figure 6d). As restoration projects have the potential to directly manipulate the diversity of planted genotypes or species, restoration ecology is uniquely placed to not only benefit from BEF theory, but to also conduct empirical tests that inform BEF theory.

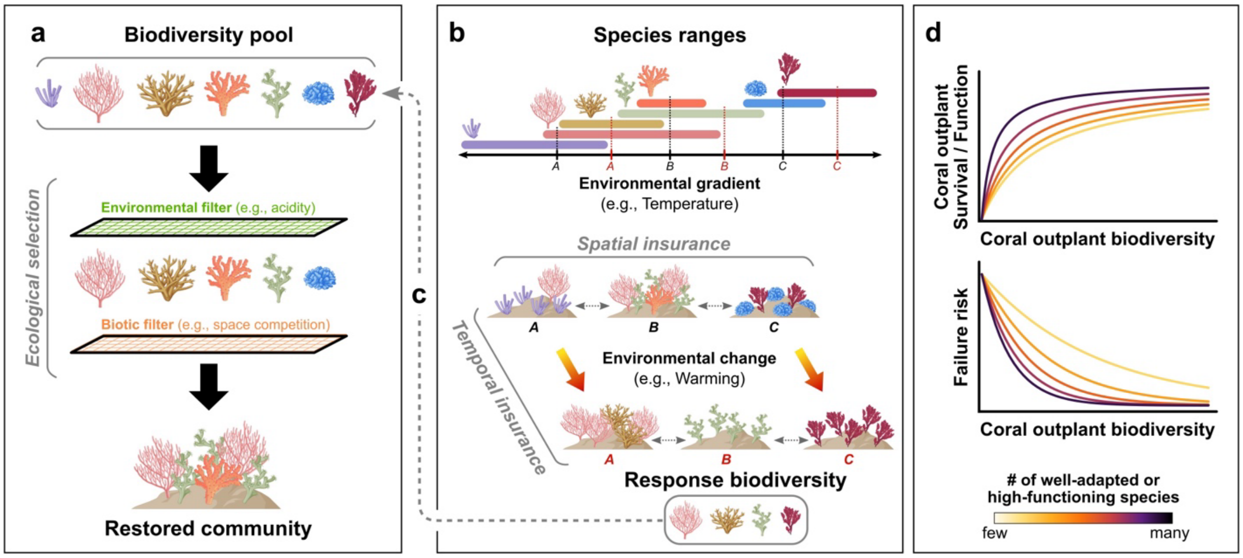

Figure 6. Effects of biodiversity on reef coral restoration success. (a) A diverse pool of candidate coral species or genotypes enhances restoration success by accounting for ecological selection of the environment and biological interactions. (b) Trait diversity (i.e., range of temperature tolerance across species) provides spatial insurance by creating variation in species/genotypic performance along environmental gradients. Response diversity provides temporal insurance by increasing the chance that some species/genotypes can tolerate environmental change. (c) Informed by initial restoration or experiments, the pool of candidate coral species can be enhanced by adding species or genotypes that can tolerate environmental change and are well-adapted. (d) Biodiversity-ecosystem function theory predicts that including more well-adapted or high-functioning species/genotypes (darker colors) can enhance restoration success by boosting (top) the positive effect of biodiversity on community survival and functioning, and reducing (bottom) failure risk.

Our <u>Top Ten List</u> of ways to harness theory to improve restoration success across many different ecosystem types:

1. Actively manage plant ecosystem restoration projects to limit destructive herbivory, either through herbivore exclusions, predator rewilding, or predator mimics.
2. Restore ecosystems with designs that harness intraspecific facilitation/ group benefits.
3. Co-restore primary and secondary facilitators to establish facilitation cascades.
4. Establish dispersal corridors within landscapes of restoration sites to increase metacommunity connectivity, encourage population establishment and persistence, increase population resistance to disturbance, and enhance species diversity.
5. Test and manage for the presence of non-linear disturbance thresholds which could plunge restorations into irrecoverable states.
6. Select a population with high trait diversity for restoration to increase resistance and resilience to different types and strengths of environmental disturbance.
7. If the restoration goal is to enhance individual growth, focus on medium to small/medium individuals. If the restoration goal is to enhance individual reproductive output, target large-bodied individuals.
8. To enhance habitat availability and biodiversity simultaneously, co-restore primary foundation species with a high abundance of functionally-distinct secondary foundation species.
9. When restoring similar habitats across a wide-latitudinal range, account for higher species richness, stronger species interactions, and higher nutrient availability in restoration sites closer to the equator.
10. Increase species diversity to simultaneously boost performance of multiple ecosystem functions and strengthen resistance and recovery from disturbance.

Box 1

Climate Change, Ecosystem Restoration, and Ecological Theory

Climate change is affecting all aspects of life across scales, from cells to ecosystems, rapidly shifting the biology and ecology of ecosystems and putting several ecological theories to the test on local, regional, and global scales. Unifying restoration and global change ecology through ecological theory, can help to chart the path forward for ecosystem management under rising CO^2 emissions and temperature. For example, food web theory, biodiversity-ecosystem function theory, and metabolic theory jointly form the theoretical background for using animal rewilding as a natural climate solution predicted to reclaim at least 0.3 $GtCO^2$/yr globally [140]. The role of top-down control becomes increasingly important under rising global temperatures –as higher trophic levels cope with increased metabolic demands associated with warmer temperatures. Restoration actions focused solely on plants or animals would then be missing a crucial aspect of climate resilience. Food web restoration to support trophic facilitation, facilitation cascades, and mutualisms will also alleviate temperature-induced species range shifts or invasions (e.g., macroalgal takeover in coral reefs)[143]. In addition, rooted in biodiversity theory, cultivating diverse communities with robust genetic makeups can enhance short- and long-term stability and increase ecosystem stress tolerance, possibly selecting for climate resistant and resilient traits [e.g., 133, 164].

Addressing climate change through restoration will hinge on future experimental tests and application of ecological theory. Identifying resistant species, discovering resilient genotypes, and optimizing methods to enhance positive interactions can mitigate climate-induced stress now, but with less-known effectiveness as climate change increases. As biogeography and metacommunity theory predict the probability of climate-resistant species colonizing new habitats, restoration can harness this knowledge through assisted migration to limit barren habitats during transition times. In fact, merging facilitation theory and resilience theory has already directed successful large-scale, climate-focused restoration in marine seagrasses and other ecosystems [98,141,142].

Lastly, a consequence of rapid climate change may be the loss of public interest in conservation and restoration. Growing accustomed to change and devastation might diminish the urgency and support for expensive restoration efforts, possibly leading to monocultures or habitat destruction [144]. However, framing this challenge during the Decade of Ecosystem Restoration uncovers the massive potential to harness ecological theory for scaled-up restoration of ecosystems across the globe. For example, as human density and climate stress increase, building ecosystems will require biogeography and metacommunity theory to anticipate future species assemblages. Additionally, the principles of biodiversity-ecosystem function theory can focus on goals that maximize ecosystem functions essential for both humans and nature. Combining our century of progress in ecological theory with this novel, intellectually expanded restoration science can substantially expand our capabilities to bring ecosystems back from the brink on a rapidly changing planet.

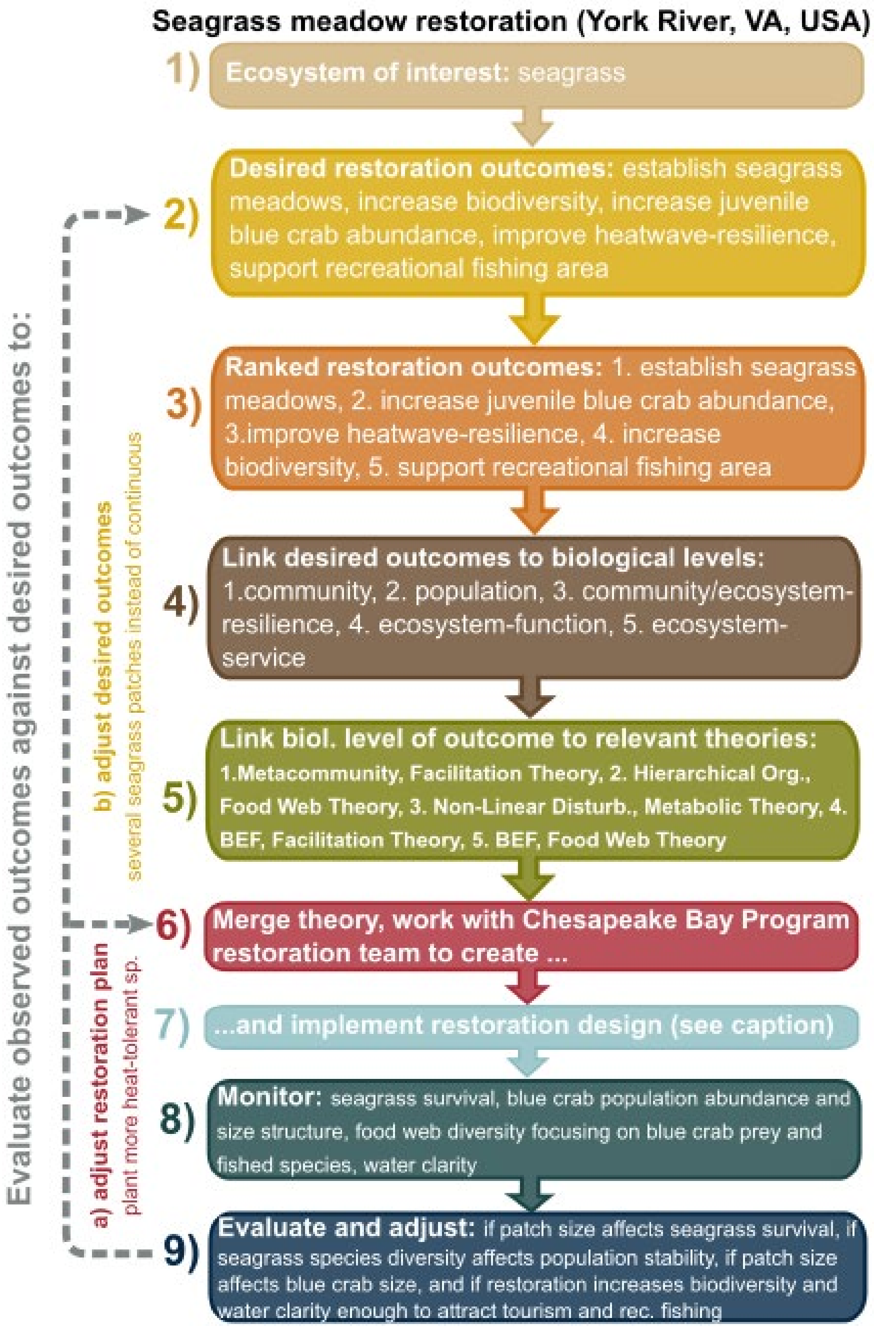

Figure 7. Harnessing theory for restoration of seagrass meadows in York River, VA. We outline an example restoration plan informed by ecological theory. The project aims to restore seagrass meadows, support nursery habitat for valuable blue crab populations, build heatwave-resistant seagrass areas, increase biodiversity, and provide areas for recreational fishing (e.g., striped bass). Based on components of ten theories that inform five restoration goals, our sample restoration plan would be co-developed with regional practitioners (step 6) and implemented (step 7) as follows: A) establish seagrass meadows by seed in 10 sites amenable to seagrass establishment; B) in each site, plant 5 large (50 x 50 m) patches, 10 medium patches (20 x 20 m) and 20 small (5 x 5 m) patches, with a 1 m wide corridor of transplanted grass connecting each patch; C) in each patch, seed both the dominant seagrass eelgrass and temperature- tolerant widgeongrass in equal abundance; D) seed or plant seedlings of widgeongrass if

marine heatwaves occur; E) add water clearing facilitators to the outside of meadows (e.g., oysters, clams); and F) protect seagrass seedlings from grazers, if detected from monitoring. Overall, a York River, VA seagrass restoration informed by theory would outplant in patches, with both short-distance and long-distance facilitators (e.g., co-plant with facilitating clams, choose sites adjacent to healthy oyster reefs, respectively). Managing herbivory *via* exclusions or predator reintroduction and employing both habitat-forming and climate-tolerant species also increases establishment success and encourages long-term stability.

Conclusion

With a survey of the relevance of 10 ecological theories to restoration and a brief case study for how to apply the framework for integrating ecological theory into restoration design (Figure 7) we present in this study how integration of different foundational ecological theories can help achieve restoration goals for biodiversity, ecosystem processes, and ultimately, landscape-scale delivery of ecosystem services (see Box 1 for our top ten list of how harnessing theory can improve restoration success across many different ecosystem types). This list of examples is far from exhaustive, and we recognize that there are other relevant theoretical frameworks that we could have mentioned, including trait-based theory and ecological network theory.

The key to fully harnessing theory for increased restoration success will be to simultaneously engage managers, ecologists, and theorists in comprehensive ecosystem restoration planning efforts. By listing all desired restoration outcomes – from taxon-specific outcomes to system-wide outcomes – multi-sector and transdisciplinary teams can evaluate which theories have the highest potential to increase success for a given project. If trade-offs are predicted (e.g., removal of an invasive plant will increase native diversity but decrease system carbon sequestration) and as restoration goals shift over time, such teams will need to work alongside stakeholders to prioritize key outcomes. Importantly, these approaches will help practitioners make decisions despite data deficiencies or uncertain baseline conditions. For ecosystem restoration to answer society's call to rebuild the world's ecosystems at the pace needed to match accelerating climatic stress and other anthropogenic pressures, we must immediately and systematically incorporate relevant ecological theory into restoration designs for all ecosystems.

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