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Review

Harnessing ecological theory to enhance ecosystem restoration

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SUMMARY

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 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 (such as 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]. These interventions have been effective in certain situations — for instance, well-managed protected areas can reverse the decline of forests and endangered species, and effective fisheries management can guard against overharvest — but these successes have not been enough. Consequently, the

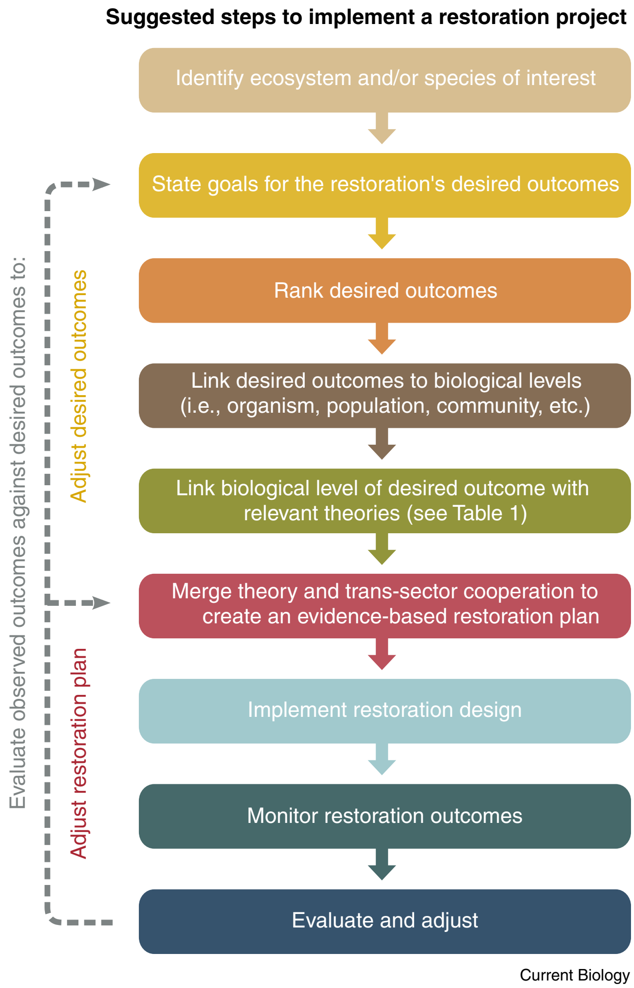

Figure 1. A flow chart for harnessing ecological theory in restoration.
Suggested steps for practitioners and ecologists to implement a restoration project together that is fully integrated with ecological theory. See Figure 7 for a worked example.

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 global sustainability and climate adaptation goals[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 an area the size of China by 2030. Yet, substantiated criticisms indicate that current restoration practices may not be up to the task because they comprise relatively expensive conservation interventions, typically small in scale and failure-prone[6]. To meet the new demands of the international community and to ultimately revitalize Earth's degraded ecosystems, restoration practice requires an increase in spatial coverage as well as several strategic, practical shifts. To address the global call for more cost-effective, scalable and successful restoration, 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 habitat has long been bolstered by predictions on the progression and trajectory of restored communities based on successional theory and community assembly theory[9,12–14]; in addition, seed-mix design for replanting was informed by coexistence theory[15,16]. Other individual ecological concepts and theories, such as facilitation, alternative stable state and landscape-ecology theory have been suggested to greatly improve restoration scale and success in aquatic[17], herbaceous plant[18] and animal-based habitat restorations[19], respectively. Yet, meta-analysis shows that successional theory and community-assembly theory continue to dominate in those limited circumstances where restoration practices have intentionally incorporated theory[20].

While the aforementioned examples offer new approaches, 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[20]. For example, fencing off plant restorations to protect outplants (i.e., nursery plants transplanted into a habitat) and seedlings from herbivores is a commonly used method that increases restored plant abundance by 89% — a stronger positive effect than managing for plant competition or physical factors[21]. Yet, even though food-web theory and its empirical tests indicate that predators have wide-reaching, strong indirect effects on plants, relatively few restoration studies incorporate predators in their design[21]. Likewise, over 100 peer-reviewed papers have called for the integration of positive species-interaction theory into coastal ecosystem restorations because facilitation-informed designs can increase success by 100–300% in marshes and seagrasses[22,23]. However, less than 3% of over 600 salt marsh, seagrass and oyster restoration studies incorporated positive species-interaction theory[24]. 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.

How to leverage theory for better habitat restoration

Here, we address this barrier by first summarizing a representative list of 10 key ecological theories that we 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 (i.e., historical or baseline conditions), the restoration approach to harness theory begins with the selection of a target ecosystem or species for the restoration (Step 1) and the setting of restoration goals

Table 1. Linking restoration outcomes with relevant theories and literature. To complete step 5 from the decision flow chart in Figure 1, practitioners and ecologists can utilize this guide to ecological theories and associated reference material.

Biological level of restoration outcome	Relevant theories	References
Gene	Evolution (e.g. selection, drift)	Rice *et al.*[152], Futuyma & Kirkpatrick[153]
	Metacommunity theory (i.e. dispersal)	Mckay *et al.*[154]
	Competition theory (intraspecific)	Leibold[155], Hartl and Clark[156]
Organism	Facilitation theory	Camazine *et al.*[157]
	Metabolic theory	Brown *et al.*[113] , Sibly *et al.*[158]
	Self-organization theory	McCann[159]
	Ecological trap theory	Hale and Swearer[160]
Population	Metapopulation theory	Maschinski and Quintana-Ascencio[161]
	Metabolic theory	Brown *et al.*[113], Savage *et al.*[162]
	Self-organization theory	Zhao *et al.*[163]
	Facilitation theory	Silliman *et al.*[22]
	R/K selection theory	MacArthur andWilson[164], Reznick *et al.*[165]
	Ecological trap theory	Hale and Swearer[160]
Community	Food web theory	Van der Zanden *et al.*[166], McCann[159]
	Facilitation theory	Gómez-Aparicio *et al.*[167]
	Metacommunity theory	Leibold *et al.*[77], Holyoak *et al.*[168]
	Neutral theory	Hubbell[169]
	Hierarchical organization through facilitation cascades	Palik *et al.*[170]
	Resilience and disturbance theory	Gunderson[171]
	Metabolic theory	Brown *et al.*[113]
	Self-organization theory	Solé and Bascompte[172]
	Coexistence theory	Chesson[173]
	Mesopredator release theory	Estes *et al.*[174]
	Competition theory (interspecific)	Bolnick *et al.*[175]
	Community assembly theory	Fukami[27]
Ecosystem-function	Facilitation theory	Gómez-Aparicio *et al.*[167], Angelini *et al.*[71]
	Metabolic theory	Brown *et al.*[113], Schramski *et al.*[176]
	Biodiversity–ecosystem function	Loreau *et al.*[140], Montoya *et al.*[177]
	Mesopredator release theory	Ritchie and Johnson[178]
Ecosystem-service	Metabolic theory	Brown *et al.*[113], Schramski *et al.*[176]
	Biodiversity–ecosystem function	Loreau et al.[140], Montoya *et al.*[177]
	Ecological systems theory	Levin[179]
Ecosystem-resilience	Hierarchical organization through facilitation cascades	Palik *et al.*[170]
	Resilience and disturbance theory	Gunderson[171]
	Metacommunity theory	Leibold *et al.*[77], Holyoak *et al.*[168]
	Biodiversity–ecosystem function (i.e., biodiversity–stability)	Loreau *et al.*[140], Montoya *et al.*[177]
	Spatial patterning through self-organization	Solé and Bascompte[172], de Paoli *et al.*[132]

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.

(Step 2). These goals are then prioritized based on stakeholder input (Step 3) and grouped by biological level of organization (e.g., population or community; 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 or target (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)[25] can be a key strategy to bypass competitive hierarchies that would otherwise suppress establishment of foundational species, such as trees or corals, that are being targeted by restoration approaches. 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, in wetland prairie restorations, direct physical removal of invasive grasses from the soil prior to restoration resets the seedbank, reduces the strength of competition for space and increases outplant growth rates and native plant diversity[26].

While managing invasion or competition to aid in restoration community assembly is becoming more common[20], 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[27]. Thus, management to prevent early-arriving species from depleting resources and to deter invaders with similar niches (niche preemption[28] or niche modification)[27,29–31] can boost establishment success. The strength and persistence of priority effects depend on the biotic and abiotic context[14], 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 that increase growth of the focal species before it comes into contact with stronger competitors[32]. Temporal priority can also be maintained through scheduled seeding or planting times to directly control the timing of both community assembly and ecosystem functioning[33]. Communication and collaboration between practitioners and experimental ecologists 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.

Food-web theory

The connectivity, diversity and evenness of producers, consumers and predators (i.e., the food-web structure) in an ecosystem control far-reaching processes. Thus, 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 has predictable bottom-up and top-down consequences. 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 or trophic position of all other organisms in the ecosystem[34,35]. 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[36,37]. From the top-down, one of the oldest ecological theories posits that the globe is green — as plants are the most abundant organisms by biomass — because predators keep herbivores in check[38,39]. Decades of experiments 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[40–43].

Food web theory has led to general predictions about trophic control in ecosystems that we argue should be part of the restoration manager repertoire: the number of trophic levels predicts plant success at the bottom of the food web, whereby odd-numbered trophic levels facilitate plants[44,45]; the number of trophic levels increases with ecosystem size in aquatic ecosystems[46] and with primary productivity in terrestrial ecosystems[47]; grazer control of plant diversity becomes stronger as plant productivity increases[21,48]; more complex food-web structure (such as higher connectivity, more trophic levels, higher within guild diversity) may enhance ecosystem resilience to invasion and disturbance[49,50]; intraspecific diversity (genetic diversity or phenotypic diversity) can influence species connectivity and trophic level[51].

Food-web theory can be systematically included in the planning stages of all restoration endeavors. By managing patch size of restored foundation species, managers can maximize initial diversity provisioning and then build new patches if diversity returns begin to diminish. 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 sites with overabundant herbivores could be strategically avoided. By managing predator presence or reintroducing locally extinct predators for enhanced herbivore control at the onset of ecosystem restoration, primary producer recovery or growth rates will improve. For example, reintroducing native predators increases the growth of outplanted terrestrial plants by ~370% on average[21]. 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 implement herbivore control creatively and manually by mimicking predator presence through herbivore exclusions and promoting non-consumptive effects (for instance, shark mimics to deter corallivorous reef fish) in areas where predator reintroduction is undesirable. By considering trophic dynamics, leveraging powerful predator–prey effects and manipulating areal coverage of foundation species, food-web theory offers a strategic approach for improving restoration establishment and functionality.

Facilitation theory

Facilitation theory-informed restoration can amplify beneficial interactions to improve establishment success and stability in stressful and highly disturbed habitats, a common ecosystem state for restorations. Positive interactions, such as facilitation or facultative and obligate mutualism, are pervasive in stressful habitats, such as alpine and prairie grasslands[52–54], the rocky intertidal zone[55,56] and salt marshes[57,58]. Indeed, the stress-gradient hypothesis[58] predicts that stress amelioration by intra- or inter-specific neighbors is more common and more important in physically and biologically harsh habitats. Additionally, reduced herbivory on individuals when adjacent to neighboring species (i.e., associational defenses) is 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 (such as microbes or habitat ameliorating neighbors) or on consumers

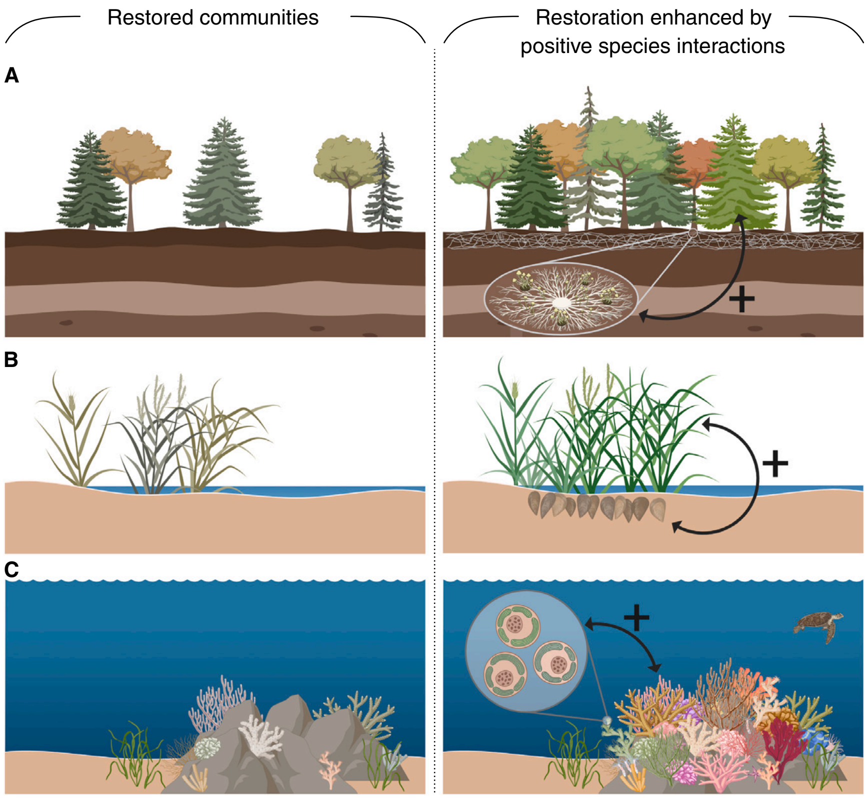

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Figure 2. Using facilitation theory to enhance restoration.
(A) Mutualisms between trees and fungal networks that distribute limiting resources improve restoration in old-growth forests. (B) Mutualisms between mussels and marsh plants reduce physical and biotic stress to enhance restoration in salt marshes. (C) Mutualisms between algal symbionts and corals underpin ecosystem development in restored coral reefs.

(such as control by predators)[17,59,60]. For example: networks of fungal mycelia distribute limiting resources among trees in old-growth forests[61] (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[22,62,63] (Figure 2B); and algal symbionts and coral neighbors underpin ecosystem development and persistence in coral reefs[64–66] (Figure 2C). Yet, management and restoration of forests, salt marshes, and coral reefs have historically ignored facilitators, only considering physical conditions and competition.

Positive species interactions that fuel productive but stressed ecosystems may increase the likelihood of restoration success in bare, degraded or destroyed habitats. In salt marsh restoration, for example, promoting intraspecific facilitation between marsh plants, by clumping outplants instead of dispersing plantings, mitigates sediment hypersalinity and anoxia to triple plant growth and survivorship[22]. Likewise, by leveraging clam fertilization on seagrass seedlings, adding clams to restoration increases seagrass propagule growth by ∼200%[67]. In restoration of denuded, semiarid plant communities, inoculation of arbuscular mycorrhizal fungi and nitrogen-fixing bacteria enhances key species establishment and ecosystem functions[68]. 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[69]. 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.

Hierarchical organization through facilitation cascades

An expansion of facilitation theory, the concept of hierarchical organization through facilitation cascades, predicts greater gains in restoration of foundation species 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[70], this integrated approach posits that physically-tolerant primary foundation species (such as 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, they also have wider-reaching, larger-scale positive effects by creating the conditions that promote secondary foundation species establishment[71]. This cascading facilitation creates more microhabitats, increased niche space and higher resource heterogeneity, all of which drive substantially higher biodiversity and ecosystem function[72–74]. 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[70]. 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.

For restoration, the hierarchical organization model predicts that restoring secondary foundation species will maximize the probability of meeting biodiversity or ecosystem service goals based on: functional and morphological dissimilarity between primary and secondary foundation species; the spatial configuration of the two foundation species; and high abundance of secondary foundation species[71,75,76] (Figure 3). Thus, for restoration

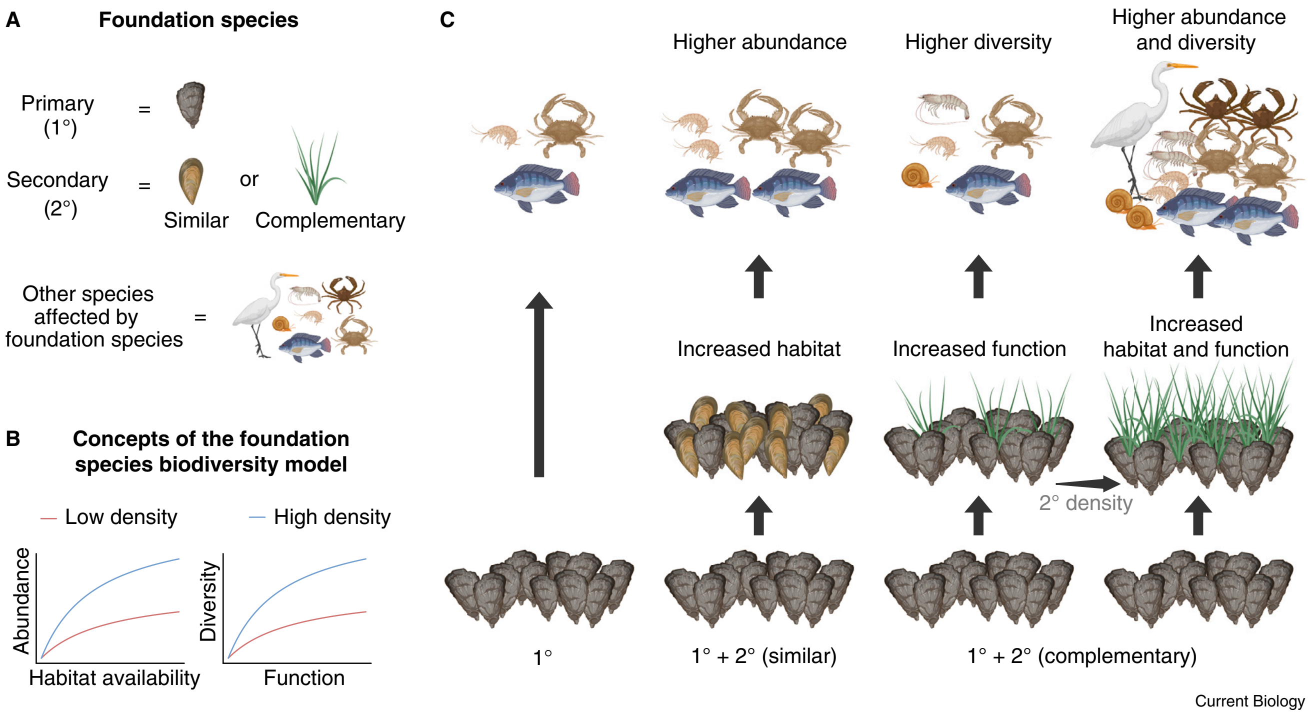

Figure 3. Using hierarchical organization theory to enhance restoration of biodiversity and ecosystem services.
(A) The hierarchical organization through facilitation cascades model distinguishes between primary (1°) and secondary (2°) foundation species. (B) Key concepts of this model are that 2° species that increase habitat availability enhance species abundances (left) and 2° species that provide additional functions increase species diversity (right). 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 with permission from[74].

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[37,76].

Metacommunity theory

For restoration of highly fragmented 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 how communities are formed and maintained across space by incorporating both the dispersal limitation and spatial processes that control extinctions and re-colonization across local, regional and global scales[77]. According to this theory, connections between local communities through dispersal can play a fundamental role in species population establishment and persistence[78], including the maintenance of genetic diversity within and across communities, which may ensure resilience to disturbance or environmental fluctuations[79]. Restoration projects could incorporate metacommunity theory in their plans to achieve recovery of populations that are both resilient to disturbance and resistant to environmental change across landscapes[80,81].

Landscape fragmentation threatens many natural habitats and restoration efforts by limiting dispersal and connectivity between communities. Careful spatial planning incorporating metacommunity dynamics includes deciding the number, size, and spatial configuration of restoration patches to manage overall connectivity among restored and remnant natural patches[82,83]. 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 successful, connectivity can be enhanced by dispersal corridors (Figure 4). Importantly, such 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[84]. On the other hand, high connectivity can be undesirable in cases where the target species are inferior competitors that may be outcompeted, for instance by invasive species, or when there are risks of disease or enemy spread[85]. In these cases, management may try to decrease connectivity, at least until the restored ecosystem has been established.

The potential of incorporating metacommunity dynamics is highlighted by the successful application of this framework in the design of California's network of Marine Protected Areas. To optimize both conservation and economic outcomes, the number, size and spacing of Marine Protected Areas were determined by models of ocean circulation, larval distance capacities, species spatial population dynamics and even fishing effort[86,87].

Nonlinear disturbance-threshold theory

For ecosystems with strong nonlinear dynamics, integrating nonlinear threshold dynamics can greatly improve restoration

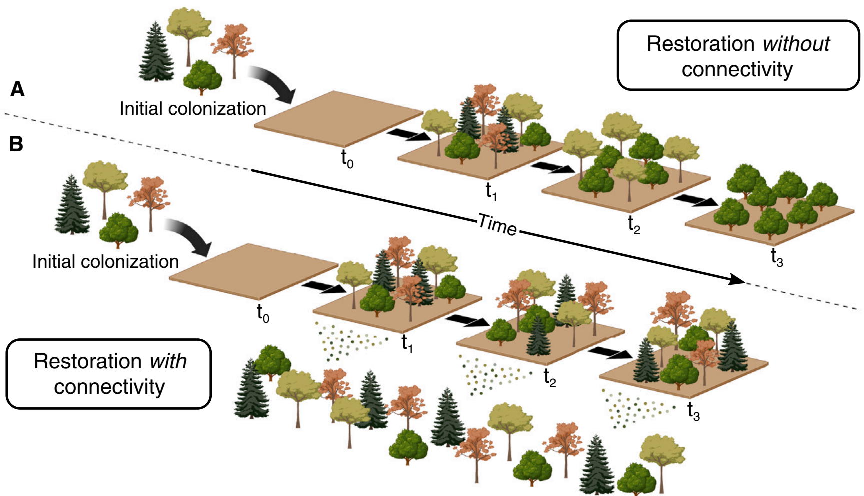

Figure 4. Effect of alternative connectivity strategies on biodiversity of restored sites.
Forest restoration over time, from degraded bare ground (t_0) to restoration initialization (t_1), over medium (t_2) and long (t_3) time scales. (A) After colonization of a restoration patch, competition, consumption/disease,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

success and efficiency. Ecosystem dynamics were long thought to change gradually and linearly with increasing frequency or strength of disturbance. These dynamics are now recognized as nonlinear, with thresholds in the level of resilience against disturbance[85]. Ecosystems may change relatively little, or even increase in diversity or productivity at low or intermediate levels of disturbance[88,89]. But, once a threshold frequency or strength of disturbance is exceeded, sudden and abrupt changes can push an ecosystem into an alternative stable state[90]. In some cases, recovery back to the previous stable state may occur at the same disturbance threshold at which collapse occurred. 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[91,92], ecologists and managers are challenged to predict ecosystem dynamics under this so-called 'hysteresis'[93]. Nonlinear threshold models with and without hysteresis can describe restored ecosystem dynamics under disturbance.

Nonlinear threshold ecosystem-dynamics have been reported in many ecosystems, such as lakes, grasslands, forests, salt marshes and coral reefs with anticipated collapses above certain thresholds of anthropogenic impacts, such as climate or land-use change[94]. 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[95]. 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. Both press disturbances (e.g., slowly increasing nutrient inputs or temperature) and pulse disturbance events (e.g., heavy rainfall events, heatwaves) can generate shifts between alternate stable states. For example, grazers can lower the tipping points of salt marshes and temperate forests to drought[96,97], overfishing can lower the tipping points of kelp forests to climate warming[98], and invasive species have been found to either lower or increase the tipping points of lake ecosystems[99].

For restoration, understanding potential thresholds can guide 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. In addition, recognizing potential thresholds can help in the management of ecological factors that modify these thresholds. Reintroduction of sea otters, for example, has allowed degraded seagrass meadows to recover despite high eutrophication levels[100]. Also, large-scale seagrass restorations (e.g., spreading seeds over a large area vs. planting individual shoots or small patches) are crucial to reach the density and area threshold at which positive feedbacks in restored meadows can stabilize sediment, lower wave action, and resist storm disturbances[101]. Overall, restoration practitioners who are aware of the ecological consequences of non-linear threshold dynamics will have a better predictive capacity for ecosystem shifts and can facilitate intervention designs that lower disturbance thresholds and improve resilience.

Biogeography and macroecology theory

When designing large-scale restoration projects, accounting for macroecological patterns in species distributions and in both top-down and bottom-up processes can help to avoid the pitfalls of a one-size-fits-all approach. Biogeographical patterns have been documented for centuries, such as Carl Linnaeus in 1735 and Georges Buffon in 1761 recording where species could be found across latitudes and longitudes[102]. Today, approaches and *post hoc* explanations rooted in biogeography theory describe how organisms and nutrients are distributed across space and time and which factors underpin these distributions[102,103]. Especially relevant to the success of restoration across large spatial scales, biogeographical patterns describe how species-interaction strength decreases with latitude and nutrient availability decreases with latitude. Predation and herbivory are suggested to be stronger in tropical regions than in temperate regions[104], evidenced by increased rates of avian nest predation[105], leaf herbivory by insects in forests[106,107], attack rates on caterpillars by arthropods[108], and herbivory in salt marshes by grasshoppers and snails[109,110]. Similarly, temperate regions are more nutrient-limited than tropical regions[111], as nutrient additions

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) and Kenya (right) successfully increase the capture and storage of water and nutrients (photos: bottom left: © Ondernemers zonder Grenzen; top left, and right: © Justdiggit).

in temperate sites create much greater increases in herbivory than in tropical sites.

These 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 or nutrient limitation than a similar restoration in a temperate zone. To mitigate this, restoration practitioners at tropical sites may consider incorporating grazer exclusion or nutrient enrichment into their designs, which would not be necessary in temperate zones. 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[112]. 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. In summary, integrating biogeography and macroecology theory into restoration designs can inform adaptable regional restoration plans that are both consistent across space and tailored to local conditions.

Metabolic theory

Metabolism builds and powers the diversity of life. The metabolic theory of ecology can inform restoration of populations, communities and ecosystem services, especially under rising temperatures. Metabolic theories view metabolism as the fundamental ecological process, complementing the central role of population dynamics in other ecological theories. Metabolic theories explain how the metabolic rates of organisms control many ecological processes by setting the rates of resource uptake and resource allocation[113]. 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. Because metabolic rate constrains rates of activities in individuals, populations, communities and ecosystems[113–115], allometries between metabolism and body size can systematically be used to predict organismal function across systems and taxa: larger systems use energy more efficiently (economy of scale)[116], while warmer systems use energy at higher rates, until they can no longer function[117]. Metabolic theory can project changes in the distribution and productivity of fish[118,119] and forests[120–122] with climate change. It has also been used to consider how microbial interactions can be included in ecosystem monitoring[123] and to predict coordinated changes in microbial community structure, dynamics and ecosystem functioning under warming[124]. 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[125].

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

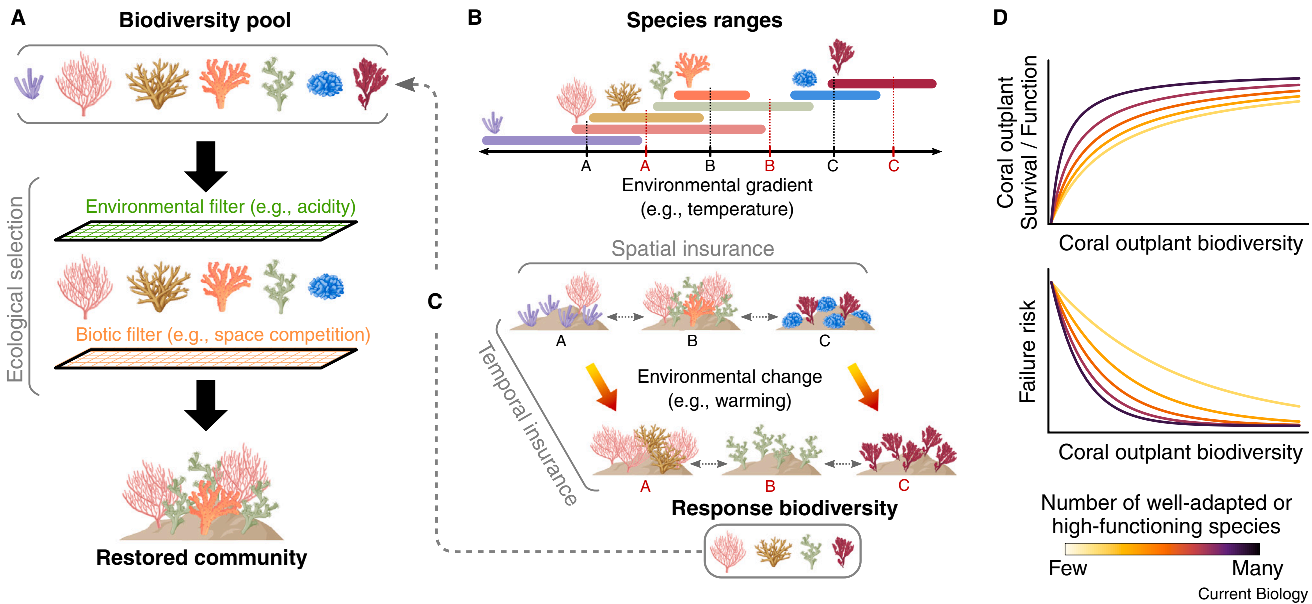

Figure 6. Effects of biodiversity on reef coral restoration success.

(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 the positive effect of biodiversity on community survival and functioning (top) and by reducing failure risk (bottom).

a broader diet than smaller animals[126]. Thus, successfully restoring large-bodied animals requires not just accounting for these increased metabolic needs but can also be enhanced by using metabolic theory to predict the size of foraging area required for healthy populations. Metabolic theory informs population and organismal-level restoration goals: if the goal of restoration is to enhance growth, focusing on small or medium individuals is recommended; if the goal is to enhance individual reproductive output, large-bodied individuals should be the focus.

In addition, metabolic theory mechanistically links metabolic rate and, thus, energetic demand, to environmental temperature[127]. Thus, restorations in areas experiencing significant anthropogenic temperature change — such as streams, forest fragments or urban landscapes — must account for increased metabolic rates and growth rates, earlier maturation and reduced lifetime reproductive outputs under warming[124]. With an increasing need to consider how restoration efforts will fare under global change, 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 restored ecosystem structure and function in a rapidly warming world[128].

Spatial patterning through self-organization

In nature, interactions between species and their environment can create coherent spatial patterns that determine ecosystem functioning and resistance to environmental change[129,130]. These patterns — e.g., biotic bands, clumps, mounds or patches in arid bushlands, forests, intertidal mussel beds, peatlands and coral reefs — are nearly ubiquitous, and can be mimicked by restoration to increase resilience to drought or storms[131]. Spatial patterning theory finds that local interactions explain the formation of large-scale spatial patterns when organisms modify their habitat to both improve their local growth conditions but inhibit conspecifics at a larger scale[131]. Importantly, post-disturbance recovery is faster if the spatial pattern remains intact or if newly-settled foundation species emulate the original spatial pattern of the system. Yet, in bare or degraded landscapes that are commonly considered for restoration, for example reclaiming landscapes homogenized by agricultural practices, the self-organized biotic spatial configuration has likely been lost. This loss of spatial structure may limit restoration efforts and make it difficult for species to gain a foothold.

The consequences of complex pattern formation may need to be accounted for in real-world restoration projects. For example, on wave-swept intertidal flats mussel restoration that imitates natural mussel band patterning increases both mussel survival and overall restoration success compared to random or equally-spaced patterning[132]. 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, African farmers successfully increase the capture and storage of water and nutrients by mimicking spatial organization[133] (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

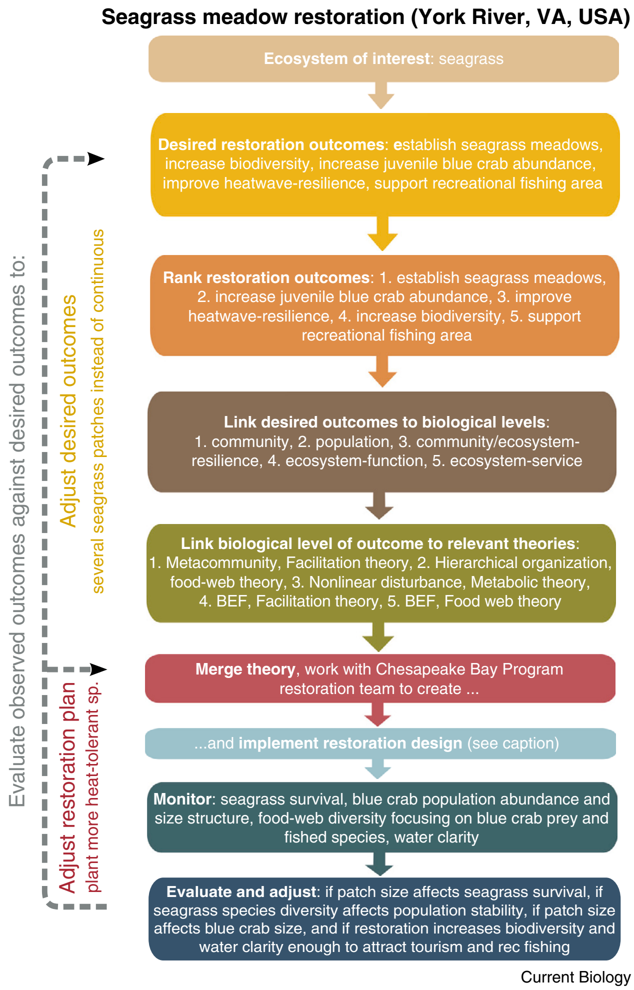

Figure 7. Harnessing theory for restoration of seagrass meadows.
We outline an example restoration plan informed by ecological theory. The project aims to restore seagrass meadows in York River, Virginia, to support nursery habitat for valuable blue crab populations, build heatwave-resistant seagrass areas, increase biodiversity and provide areas for recreational fishing (e.g., striped bass). Based on components of seven 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: establish seagrass meadows by seed in 10 sites amenable to seagrass establishment; 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; in each patch, seed both the dominant seagrass eelgrass and temperature-tolerant widgeongrass in equal abundance; seed or plant seedlings of widgeongrass if marine heatwaves occur; add water clearing facilitators to the outside of meadows (e.g., oysters, clams); and protect seagrass seedlings from grazers, if detected from monitoring. Overall, 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.

spatial patterns originating from self-organized spatial pattern formation[133,134].

Biodiversity–ecosystem functioning theory

Biodiversity–ecosystem function theory makes valuable predictions that may enhance restoration outcomes across a hierarchy of scales. The diversity of life, across ecosystems and trophic levels, enhances ecological processes. Biodiversity–ecosystem functioning theory posits that the diversity of species, functional traits or genetics consistently increases ecosystem functioning and its stability over time[135]. Intraspecific diversity also supports processes important to restoration; within-organism trait or genetic diversity increases population survival and growth, while within-population trait or genetic diversity increases resistance and resilience to disturbance[136]. Biodiversity enhances broad ecosystem processes through either the stabilizing benefits associated with having multiple species that can perform similar ecological roles (functional redundancy) or the benefits associated with having a suite of species that perform different roles (functional niche complementarity). Biodiversity enhances ecosystem function by both mechanisms and can also enhance restoration outcomes by both mechanisms.

At individual restoration sites, trait diversity, for instance planting trees of different sizes, will promote functional niche complementarity, facilitation and trophic feedbacks[137,138]. Furthermore, trait diversity provides the raw material for natural 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[139]. Next, across restoration sites in a region, increasing species or trait diversity creates community and population-level niche differences that can both maximize resource uptake and survival probability[140] (Figure 6B). Across land- and seascapes with multiple ecosystem types, restoring with a diverse set of species also optimizes restoration success because, given adequate dispersal opportunities, species will dominate the habitats in which they are best suited[140]. Biodiversity also provides temporal insurance: the differential, asynchronous responses to environmental gradients or disturbance that diversity provides can protect restoration projects from climatic extremes[141]. With climate-induced range shifts, managers can even utilize the changing regional biodiversity pool to bolster response diversity, as climate migrants may provide stability during times of high community turnover (Figure 6C). Although there is evidence for such spatiotemporal insurance effects in real communities[142], these mechanisms can be disrupted by certain competitive interactions, stochastic processes or extreme levels of connectivity and dispersal.

Theory and evidence indicate that integrating biodiversity is an indispensable asset to restoration programs expanding in scale and facing accelerating climate change[143,144]. Given information on species traits and natural history, managers may be able to tailor species composition to best capitalize on known mechanisms of complementarity over space and time. Yet, uncertain responses of species to multiple and novel stressors means that embracing biodiversity is a prudent 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 highly 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 biodiversity–ecosystem function theory, but also to conduct empirical tests that inform this theory.

Box 1. Our top ten ways to harness theory to improve restoration.

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 or 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 as well as enhance species diversity.
5. Test and manage 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 small/medium-size 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.

Ecosystem restoration, ecological theory and climate change

Because climate change is rapidly shifting the biology and ecology of ecosystems, ecological theory-guided restoration is now more relevant than ever. Harnessing theory can help chart a path forward for the new ecosystem management strategies needed to counter rising CO_2 emissions. 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 to enhance carbon capture and storage in ecosystems around the globe[145]. Restoration actions focused solely on plants or animals would then be missing a crucial aspect of climate resilience. Theoretical predictions also highlight specific strategies that need to be adapted under different climates. For example, the role of top-down control becomes more important under rising global temperatures as higher trophic levels have to cope with increased metabolic demands associated with warmer temperatures. Food web restoration to support trophic facilitation, facilitation cascades, and mutualisms can also alleviate temperature-induced species range shifts or invasions (e.g., macroalgal takeover in coral reefs)[146]. In addition, rooted in biodiversity theory, cultivating diverse communities with robust genetic makeups can enhance short- and long-term stability and increase climate stress tolerance, possibly selecting for both resistant and resilient traits[144,147,148]. Forward-facing restoration can also harness biogeography and metacommunity theory predictions on colonization probabilities and use 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[101,149,150]. Into the future, addressing climate change through restoration will hinge on future experimental tests and application of ecological theory to identify resistant species, discover resilient genotypes and optimize methods to enhance positive interactions.

Lastly, a consequence of rapid climate change may be the loss of public interest in conservation and restoration. Growing accustomed to change, devastation, and unsuccessful small-scale restorations might diminish the urgency and support for expensive restoration efforts, possibly leading to monocultures or habitat destruction[151]. However, framing this challenge during the Decade of Ecosystem Restoration when investment in restoration is high uncovers a 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. Thus, climate-ready restorations of adaptable, tolerant species can be prioritized instead of replanting doomed species already near environmental limits. Additionally, the principles of non-linear disturbance threshold and biodiversity–ecosystem function theory can focus on goals that maximize ecosystem functions essential for both humans and nature under new disturbance regimes. For example, living shoreline restorations, nature-based infrastructure used to stabilize shorelines, can be designed with these theories to form networks along a coastline that simultaneously maximize coastal protection, water quality and fisheries habitat for a community, city or region. Combining our century of progress in ecological theory with intellectually expanded restoration science can build public support and substantially expand our capabilities to bring ecosystems back from the brink on a rapidly changing planet.

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 have reviewed how integration of different foundational ecological theories can help achieve restoration goals for biodiversity and ecosystem processes and services (Box 1). This list of theories 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 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 — for instance when 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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DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Cairns, J., and Heckman, J.R. (1996). Restoration ecology: The state of an emerging field. Annu. Rev. Energy Environ. *21*, 167–189. https://doi.org/10.1146/annurev.energy.21.1.167.
2. Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E. a, Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., *et al*. (2010). Global biodiversity: indicators of recent declines. Science *328*, 1164–1168. https://doi.org/10.1126/science.1187512.
3. Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., and Wilmshurst, J.M. (2017). Biodiversity losses and conservation responses in the Anthropocene. Science *356*, 270–275. https://doi.org/10.1126/science.aam9317.
4. Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H.M., Leadley, P.W., Regan, E.C., and Alkemade, R. (2014). A mid-term analysis of progress toward international biodiversity targets. Science *346*, 241–244. https://doi.org/10.1126/science.1257484.
5. Programme, U.N.E. (2021). UN Decade on Ecosystem Restoration 2021–2030: Terms of Reference of the Science Task Force.
6. Bayraktarov, E., Saunders, M.I., Abdullah, S., Mills, M., Beher, J., Possingham, H.P., Mumby, P.J., and Lovelock, C.E. (2016). The cost and feasibility of marine coastal restoration. Ecol. Appl. *26*, 1055–1074. https://doi.org/10.1890/15-1077.
7. Bradshaw, A.D. (1987). Restoration: the acid test for ecology. In Restoration Ecology: A Synthetic Approach to Ecological Research, G. Jordan, M.E., and J.D. Aber, eds. (Cambridge: Cambridge University Press), pp. 23–29.
8. Greipsson, S. (2011). Restoration Ecology (Sudbury, MA: Jones and Bartlett).
9. Palmer, M.A., Ambrose, R.F., and Poff, N.L. (1997). Ecological theory and community restoration ecology. Restor. Ecol. *5*, 291–300. https://doi.org/10.1046/j.1526-100X.1997.00543.x.
10. Falk, D.A., Palmer, M.A., and Zedler, J.B. (2006). In Foundations of Restoration Ecology (Washngton DC: Island Press).
11. Van Andel, J., and Aronson, J. (2012). Restoration Ecology: The New Frontier, 1st edn. (Oxford: Wiley). https://doi.org/10.1002/9781118223130.
12. Werden, L.K., Calderón-Morales, E., Alvarado, J.P., Gutiérrez, L.M., Nedveck, D.A., and Powers, J.S. (2020). Using large-scale tropical dry forest restoration to test successional theory. Ecol. Appl. *30*, e02116. https://doi.org/10.1002/eap.2116.
13. Cargill, S.M., and Chapin, F.S., III. (1987). Application of successional theory to tundra restoration: A review. Arctic Alpine Res. *19*, 366. https://doi.org/10.2307/1551401.
14. Young, T.P., Chase, J.M., and Huddleston, R.T. (2001). Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. Ecol. Restor. *19*, 5–18.
15. Kraft, N.J.B., Godoy, O., and Levine, J.M. (2015). Plant functional traits and the multidimensional nature of species coexistence. Proc. Natl. Acad. Sci. USA *112*, 797–802. https://doi.org/10.1073/pnas.1413650112.
16. Meissen, J.C., Glidden, A.J., Sherrard, M.E., Elgersma, K.J., and Jackson, L.L. (2020). Seed mix design and first year management influence multifunctionality and cost-effectiveness in prairie reconstruction. Restor. Ecol. *28*, 807–816. https://doi.org/10.1111/rec.13013.
17. Halpern, B.S., Silliman, B.R., Olden, J.D., Bruno, J.P., and Bertness, M.D. (2007). Incorporating positive interactions in aquatic restoration and conservation. Front. Ecol. Environ. *5*, 153–160.
18. Suding, K.N., Gross, K.L., and Houseman, G.R. (2004). Alternative states and positive feedbacks in restoration ecology. Trends Ecol. Evol. *19*, 46–53. https://doi.org/10.1016/j.tree.2003.10.005.
19. Gilby, B.L., Olds, A.D., Connolly, R.M., Henderson, C.J., and Schlacher, T.A. (2018). Spatial restoration ecology: Placing restoration in a landscape context. BioScience *68*, 1007–1019. https://doi.org/10.1093/biosci/biy126.
20. Wainwright, C.E., Staples, T.L., Charles, L.S., Flanagan, T.C., Lai, H.R., Loy, X., Reynolds, V.A., and Mayfield, M.M. (2018). Links between community ecology theory and ecological restoration are on the rise. J. Appl. Ecol. *55*, 570–581. https://doi.org/10.1111/1365-2664.12975.
21. Xu, C., Silliman, B.R., Chen, J., Li, X., Thomsen, M.S., Zhang, Q., Lee, J., Lefcheck, J.S., Daleo, P., Hughes, B.B., *et al*. (2023). Herbivory limits success of vegetation restoration globally. Science *382*, 589–594. https://doi.org/10.1126/science.add2814.
22. Silliman, B.R., Schrack, E., He, Q., Cope, R., Santoni, A., van der Heide, T., Jacobi, R., Jacobi, M., and van de Koppel, J. (2015). Facilitation shifts paradigms and can amplify coastal restoration efforts. Proc. Natl. Acad. Sci. USA *112*, 14295–14300. https://doi.org/10.1073/pnas.1515297112.
23. Zhang, Y.S., Gittman, R.K., Donaher, S.E., Trackenberg, S.N., Heide, T., and Silliman, B.R. (2021). Inclusion of intra- and interspecific facilitation expands the theoretical framework for seagrass restoration. Front. Mar. Sci *8*, 296. https://doi.org/10.3389/fmars.2021.645673.
24. Zhang, Y., Cioffi, W., Cope, R., Daleo, P., Heywood, E., Hoyt, C., Smith, C., and Silliman, B. (2018). A global synthesis reveals gaps in coastal habitat restoration research. Sustainability *10*, 1040. https://doi.org/10.3390/10041040.
25. Alford, R.A., and Wilbur, H.M. (1985). Priority effects in experimental pond communities: Competition between Bufo and Rana. Ecology *66*, 1097–1105. https://doi.org/10.2307/1939161.
26. Pfeifer-Meister, L., Johnson, B.R., Roy, B.A., Carreño, S., Stewart, J.L., and Bridgham, S.D. (2012). Restoring wetland prairies: tradeoffs among native plant cover, community composition, and ecosystem functioning. Ecosphere *3*, 1–19. https://doi.org/10.1890/ES12-00261.1.

27. Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annu. Rev. Ecol. Evol. Syst. *46*, 1–23. https://doi.org/10.1146/annurev-ecolsys-110411-160340.

28. Shea, K., and Chesson, P. (2002). Community ecology theory as a framework for biological invasions. Trends Ecol. Evol. *17*, 170–176. https://doi.org/10.1016/s0169-5347(02)02495-3.

29. Medina-Villar, S., Uscola, M., Pérez-Corona, M.E., and Jacobs, D.F. (2020). Environmental stress under climate change reduces plant performance, yet increases allelopathic potential of an invasive shrub. Biol. Invasions *22*, 2859–2881. https://doi.org/10.1007/s10530-020-02286-6.

30. Vilà, M., and Weiner, J. (2004). Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. Oikos *105*, 229–238. https://doi.org/10.1111/j.0030-1299.2004.12682.x.

31. Waller, L.P., Allen, W.J., Barratt, B.I.P., Condron, L.M., França, F.M., Hunt, J.E., Koele, N., Orwin, K.H., Steel, G.S., and Tylianakis, J.M. (2020). Biotic interactions drive ecosystem responses to exotic plant invaders. Science *368*, 967–972. https://doi.org/10.1126/science.aba2225.

32. Porensky, L.M., Vaughn, K.J., and Young, T.P. (2012). Can initial intraspecific spatial aggregation increase multi-year coexistence by creating temporal priority? Ecol. Appl. *22*, 927–936. https://doi.org/10.1890/11-0818.1.

33. Weidlich, E.W.A., Nelson, C.R., Maron, J.L., Callaway, R.M., Delory, B.M., and Temperton, V.M. (2021). Priority effects and ecological restoration. Restor. Ecol. *29*, 13317. https://doi.org/10.1111/rec.13317.

34. Bruno, J.F., and Bertness, M.D. (2001). Habitat modification and facilitation in benthic marine communities. In Marine Community Ecology, M.D. Bertness, S. Gaines, and M. Hay, eds. (Sunderland, MA: Sinauer), pp. 201–216.

35. Borst, A.C.W., Verberk, W.C.E.P., Angelini, C., Schotanus, J., Wolters, J.-W., Christianen, M.J.A., van der Zee, E.M., Derksen-Hooijberg, M., and van der Heide, T. (2018). Foundation species enhance food web complexity through non-trophic facilitation. PLoS One *13*, 199152. https://doi.org/10.1371/journal.pone.0199152.

36. Rohr, J.R., Mahan, C.G., and Kim, K.C. (2009). Response of arthropod biodiversity to foundation species declines: The case of the eastern hemlock. For. Ecol. Manag. *258*, 1503–1510. https://doi.org/10.1016/j.foreco.2009.07.002.

37. Thomsen, M.S., Altieri, A.H., Angelini, C., Bishop, M.J., Bulleri, F., Farhan, R., Frühling, V.M.M., Gribben, P.E., Harrison, S.B., and He, Q. (2022). Heterogeneity within and among co-occurring foundation species increases biodiversity. Nat. Commun. *13*, 581. https://doi.org/10.1038/s41467-022-28194-y.

38. Hariston, N.G., Smith, F.E., and Slobodkin, L.B. (1960). Community structure, population control, and competition. Am. Nat. *94*, 421–425.

39. Bar-On, Y.M., Phillips, R., and Milo, R. (2018). The biomass distribution on Earth. Proc. Natl. Acad. Sci. USA *115*, 6506–6511. https://doi.org/10.1073/pnas.1711842115.

40. Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D., and Halpern, B.S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. Ecol. Lett. *5*, 785–791. https://doi.org/10.1046/j.1461-0248.2002.00381.x.

41. Connell, J.H. (1970). A predator-prey system in the marine intertidal region. I. Balanus glandula and several predatory species of Thais. Ecol. Monogr. *40*, 49–78. https://doi.org/10.2307/1942441.

42. Dayton, P.K. (1971). Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. *41*, 351–389. https://doi.org/10.2307/1948498.

43. Paine, R. (1966). Food web complexity and species diversity. Am. Nat. *100*, 65–75.

44. Hairston, N.G., and Hairston, N.G. (1993). Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. Am. Nat. *142*, 379–411. https://doi.org/10.1086/285546.

45. Hughes, B.B., Beheshti, K.M., Tinker, M.T., Angelini, C., Endris, C., Murai, L., Anderson, S.C., Espinosa, S., Staedler, M., Tomoleoni, J.A., *et al*. (2024). Top-predator recovery abates geomorphic decline of a coastal ecosystem. Nature *626*, 111–118. https://doi.org/10.1038/s41586-023-06959-9.

46. Post, D.M., Pace, M.L., and Hairston, N.G. (2000). Ecosystem size determines food-chain length in lakes. Nature *405*, 1047–1049. https://doi.org/10.1038/35016565.

47. Young, H.S., McCauley, D.J., Dunbar, R.B., Hutson, M.S., Ter-Kuile, A.M., and Dirzo, R. (2013). The roles of productivity and ecosystem size in determining food chain length in tropical terrestrial ecosystems. Ecology *94*, 692–701. https://doi.org/10.1890/12-0729.1.

48. Olff, H., and Ritchie, M.E. (1998). Effects of herbivores on grassland plant diversity. Trends Ecol. *Evol 13*, 261–265.

49. Allesina, S., and Tang, S. (2012). Stability criteria for complex ecosystems. Nature *483*, 205–208. https://doi.org/10.1038/nature10832.

50. May, R.M. (1972). Will a large complex system be stable? Nature *238*, 413–414. https://doi.org/10.1038/238413a0.

51. Gibert, J.P., and DeLong, J.P. (2017). Phenotypic variation explains food web structural patterns. Proc. Natl. Acad. Sci. USA *114*, 11187–11192. https://doi.org/10.1073/pnas.1703864114.

52. Callaway, R.M., Nadkarni, N.M., and Mahall, B.E. (1991). Facilitation and interference of Quercus Douglasii on understory productivity in central California. Ecology *72*, 1484–1499. https://doi.org/10.2307/1941122.

53. McNaughton, S.J. (1976). Serengeti migratory wildebeest: Facilitation of energy flow by grazing. Science *191*, 92–94. https://doi.org/10.1126/science.191.4222.92.

54. Tilman, D., and Downing, J.A. (1994). Biodiversity and stability in grasslands. Nature *367*, 363–365. https://doi.org/10.1038/367363a0.

55. Dayton, P.K. (1975). Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. *45*, 137–159. https://doi.org/10.2307/1942404.

56. Bertness, M.D. (1989). Intraspecific competition and facilitation in a northern acorn barnacle population. Ecology *70*, 257–268. https://doi.org/10.2307/1938431.

57. Bertness, M.D. (1984). Habitat and community modification by an introduced herbivorous snail. Ecology *65*, 370–381.

58. Bertness, M.D., and Callaway, R. (1994). Positive interactions in communities. Trends Ecol. Evol. *9*, 191–193. https://doi.org/10.1016/0169-5347(94)90088-4.

59. Harris, J. (2009). Soil microbial communities and restoration ecology: Facilitators or followers? Science *325*, 573–574. https://doi.org/10.1126/science.1172975.

60. Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G., and McDonald, R.A. (2012). Ecosystem restoration with teeth: what role for predators? Trends Ecol. Evol. *27*, 265–271. https://doi.org/10.1016/j.tree.2012.01.001.

61. Selosse, M.-A., Richard, F., He, X., and Simard, S.W. (2006). Mycorrhizal networks: des liaisons dangereuses? Trends Ecol. Evol. *21*, 621–628. https://doi.org/10.1016/j.tree.2006.07.003.

62. Bertness, M.D., and Leonard, G.H. (1997). The role of positive interactions in communities: lessons from intertidal habitats. Ecology *78*, 1976–1989.

63. Angelini, C., Griffin, J.N., van de Koppel, J., Lamers, L.P.M., Smolders, A.J.P., Derksen-Hooijberg, M., van der Heide, T., and Silliman, B.R. (2016). A keystone mutualism underpins resilience of a coastal ecosystem to drought. Nat. Commun. *7*, 12473. https://doi.org/10.1038/ncomms12473.

64. Clements, C.S., and Hay, M.E. (2019). Biodiversity enhances coral growth, tissue survivorship and suppression of macroalgae. Nat. Ecol. Evol. *3*, 178–182. https://doi.org/10.1038/s41559-018-0752-7.

65. Ladd, M.C., Miller, M.W., Hunt, J.H., Sharp, W.C., and Burkepile, D.E. (2018). Harnessing ecological processes to facilitate coral restoration. Front. Ecol. Environ. *16*, 239–247. https://doi.org/10.1002/fee.1792.

66. Shaver, E.C., and Silliman, B.R. (2017). Time to cash in on positive interactions for coral restoration. PeerJ *5*, e3499. https://doi.org/10.7717/peerj.3499.

67. Zhang, Y.S., and Silliman, B.R. (2019). A facilitation cascade enhances local biodiversity in seagrass beds. Diversity *11*, 30. https://doi.org/10.3390/11030030.

68. Requena, N., Perez-Solis, E., Azcón-Aguilar, C., Jeffries, P., and Barea, J.-M. (2001). Management of indigenous plant-microbe symbioses aids restoration of desertified ecosystems. Appl. Environ. Microbiol. *67*, 495–498. https://doi.org/10.1128/AEM.67.2.495-498.2001.

69. Farrer, E.C., Van Bael, S.A., Clay, K., and Smith, M.K.H. (2022). Plant-microbial symbioses in coastal systems: Their ecological importance and role in coastal restoration. Estuaries Coasts *45*, 1805–1822. https://doi.org/10.1007/s12237-022-01052-2.

70. Altieri, A.H., Silliman, B.R., and Bertness, M.D. (2007). Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. Am. Nat. *169*, 195–206. https://doi.org/10.1086/510603.

71. Angelini, C., Altieri, A.H., Silliman, B.R., and Bertness, M.D. (2011). Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience *61*, 782–789. https://doi.org/10.1525/bio.2011.61.10.8.

72. Thomsen, M.S., Altieri, A.H., Angelini, C., Bishop, M.J., Gribben, P.E., Lear, G., He, Q., Schiel, D.R., Silliman, B.R., South, P.M., *et al*. (2018). Secondary foundation species enhance biodiversity. Nat. Ecol. Evol. *2*, 634–639. https://doi.org/10.1038/s41559-018-0487-5.

73. van der Zee, E.M., Angelini, C., Govers, L.L., Christianen, M., Altieri, A.H., van der Reijden, K.J., Silliman, B.R., van de Koppel, J., Van der Geest, M., van Gils, J. a, *et al*. (2016). How habitat-modifying organisms structure the food web of two coastal ecosystems. Proc. Biol. Sci. *283*, 20152326. https://doi.org/10.1098/rspb.2015.2326.

74. Yakovis, E., and Artemieva, A. (2017). Cockles, barnacles and ascidians compose a subtidal facilitation cascade with multiple hierarchical levels of foundation species. Sci. Rep. *7*, 237. https://doi.org/10.1038/s41598-017-00260-2.

75. Gribben, P.E., Angelini, C., Altieri, A.H., Bishop, M.J., Thomsen, M.S., and Bulleri, F. (2019). Facilitation cascades in marine ecosystems: A synthesis and future directions. In Oceanography and Marine Biology, S.J. Hawkins, A.L. Allcock, A.E. Bates, L.B. Firth, I.P. Smith, S.E. Swearer, and P.A. Todd, eds. (Boca Raton: CRC Press), pp. 127–168. https://doi.org/10.1201/9780429026379-3.

76. Angelini, C., and Silliman, B.R. (2014). Secondary foundation species as drivers of trophic and functional diversity: Evidence from a tree-epiphyte system. Ecology *95*, 185–196. https://doi.org/10.1890/13-0496.1.

77. Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., *et al*. (2004). The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. *7*, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x.

78. Leibold, M.A., Chase, J.M., and Ernest, S.K.M. (2017). Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes. Ecology *98*, 909–919. https://doi.org/10.1002/ecy.1697.

79. Griffiths, S.M., Taylor-Cox, E.D., Behringer, D.C., Butler, M.J., and Preziosi, R.F. (2020). Using genetics to inform restoration and predict resilience in declining populations of a keystone marine sponge. Biodivers. Conserv. *29*, 1383–1410. https://doi.org/10.1007/s10531-020-01941-7.

80. Driscoll, D.A., Banks, S.C., Barton, P.S., Ikin, K., Lentini, P., Lindenmayer, D.B., Smith, A.L., Berry, L.E., Burns, E.L., and Edworthy, A. (2014). The trajectory of dispersal research in conservation biology. Systematic review. PLoS One *9*, 95053. https://doi.org/10.1371/journal.pone.0095053.

81. Puckett, B.J., Eggleston, D.B., Kerr, P.C., and Luettich, R.A. (2014). Larval dispersal and population connectivity among a network of marine reserves. Fish. Oceanogr. *23*, 342–361. https://doi.org/10.1111/fog.12067.

82. Gawecka, K.A., and Bascompte, J. (2023). Habitat restoration and the recovery of metacommunities. J. Appl. Ecol. *60*, 1622–1636. https://doi.org/10.1111/1365-2664.14445.

83. Lester, S.E., Dubel, A.K., Hernán, G., McHenry, J., and Rassweiler, A. (2020). Spatial planning principles for marine ecosystem restoration. Front. Mar. Sci. *7*, 328.

84. Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., Danielson, B.J., Brinkerhoff, J., Damschen, E.I., and Townsend, P. (2002). Corridors affect plants, animals, and their interactions in fragmented landscapes. Proc. Natl. Acad. Sci. USA *99*, 12923–12926. https://doi.org/10.1073/pnas.202242699.

85. Brown, B.L., and Barney, J.N. (2021). Rethinking biological invasions as a metacommunity problem. Front. Ecol. Evol. *8*, 584701.

86. Gleason, M., Fox, E., Ashcraft, S., Vasques, J., Whiteman, E., Serpa, P., Saarman, E., Caldwell, M., Frimodig, A., and Miller-Henson, M. (2013). Designing a network of marine protected areas in California: Achievements, costs, lessons learned, and challenges ahead. Ocean Coast. Manag. *74*, 90–101. https://doi.org/10.1016/j.ocecoaman.2012.08.013.

87. Murray, S., and Hee, T.T. (2019). A rising tide: California's ongoing commitment to monitoring, managing and enforcing its marine protected areas. Ocean Coast. Manag. *182*, 104920. https://doi.org/10.1016/j.ocecoaman.2019.104920.

88. Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. Science *199*, 1302–1310.

89. Fox, J.W. (2013). The intermediate disturbance hypothesis should be abandoned. Trends Ecol. Evol. *28*, 86–92. https://doi.org/10.1016/j.tree.2012.08.014.

90. Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. Nature *413*, 591–596. https://doi.org/10.1038/35098000.

91. Lever, J.J., Van Nes, E.H., Scheffer, M., and Bascompte, J. (2014). The sudden collapse of pollinator communities. Ecol. Lett. *17*, 350–359. https://doi.org/10.1111/ele.12236.

92. van der Heide, T., Angelini, C., De Fouw, J., and Eklöf, J.S. (2021). Facultative mutualisms: A double-edged sword for foundation species in the face of anthropogenic global change. Ecol. Evol. *11*, 29–44. https://doi.org/10.1002/ece3.7044.

93. Beisner, B.E., Haydon, D.T., and Cuddington, K. (2003). Alternative stable states in ecology. Front. Ecol. Environ. *1*, 376–382.

94. Dakos, V., Matthews, B., Hendry, A.P., Levine, J., Loeuille, N., Norberg, J., Nosil, P., Scheffer, M., and Meester, L. (2019). Ecosystem tipping points in an evolving world. Nat. Ecol. Evol. *3*, 355–362. https://doi.org/10.1038/s41559-019-0797-2.

95. Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., Nes, E.H., Rietkerk, M., and Sugihara, G. (2009). Early-warning signals for critical transitions. Nature *461*, 53–59. https://doi.org/10.1038/nature08227.

96. He, Q., Silliman, B.R., and Cui, B. (2017). Incorporating thresholds into understanding salinity tolerance: A study using salt-tolerant plants in salt marshes. Ecol. Evol. *7*, 6326–6333. https://doi.org/10.1002/ece3.3209.

97. Silliman, B.R., van de Koppel, J., Bertness, M.D., Stanton, L.E., and Mendelssohn, I.a (2005). Drought, snails, and large-scale die-off of southern U.S. salt marshes. Science *310*, 1803–1806. https://doi.org/10.1126/science.1118229.

98. Ling, S.D. (2008). Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. Oecologia *156*, 883–894. https://doi.org/10.1007/s00442-008-1043-9.

99. Reynolds, S.A., and Aldridge, D.C. (2021). Global impacts of invasive species on the tipping points of shallow lakes. Glob. Change Biol. *27*, 6129–6138. https://doi.org/10.1111/gcb.15893.

100. Hughes, B.B., Eby, R., Van Dyke, E., Tinker, M.T., Marks, C.I., Johnson, K.S., and Wasson, K. (2013). Recovery of a top predator mediates negative eutrophic effects on seagrass. Proc. Natl. Acad. Sci. USA *110*, 15313–15318. https://doi.org/10.1073/pnas.1302805110.

101. van Katwijk, M.M., Thorhaug, A., Marbà, N., Orth, R.J., Duarte, C.M., Kendrick, G.A., Althuizen, I.H.J., Balestri, E., Bernard, G., Cambridge, M.L., *et al*. (2016). Global analysis of seagrass restoration: the importance of large-scale planting. J. Appl. Ecol. *53*, 567–578. https://doi.org/10.1111/1365-2664.12562.

102. Cox, C.B., Moore, P.D., and Ladle, R.J. (2016). Biogeography: An Ecological and Evolutionary Approach (Chichester: John Wiley & Sons).

103. Ball, I.R. (1975). Nature and formulation of biogeographical hypotheses. Syst. Biol. *24*, 407–430. https://doi.org/10.1093/sysbio/24.4.407.

104. Moles, A.T., Bonser, S.P., Poore, A.G.B., Wallis, I.R., and Foley, W.J. (2011). Assessing the evidence for latitudinal gradients in plant defence and herbivory. Funct. Ecol. *25*, 380–388. https://doi.org/10.1111/j.1365-2435.2010.01814.x.

105. Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M., and Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? Annu. Rev. Ecol. Evol. Syst. *40*, 245–269. https://doi.org/10.1146/annurev.ecolsys.39.110707.173430.

106. Adams, J.M., Zhang, Y., Basri, M., and Shukor, N. (2009). Do tropical forest leaves suffer more insect herbivory? A comparison of tropical versus temperate herbivory, estimated from leaf litter. Ecol. Res. *24*, 1381–1392. https://doi.org/10.1007/s11284-009-0623-4.

107. Zhang, Y., Adams, J., and Zhao, D. (2011). Does insect folivory vary with latitude among temperate deciduous forests? Ecol. Res. *26*, 377–383. https://doi.org/10.1007/s11284-010-0792-1.

108. Roslin, T., Hardwick, B., Novotny, V., Petry, W.K., Andrew, N.R., Asmus, A., Barrio, I.C., Basset, Y., Boesing, A.L., and Bonebrake, T.C. (2017). Higher predation risk for insect prey at low latitudes and elevations. Science *356*, 742–744. https://doi.org/10.1126/science.aaj1631.

109. Pennings, S.C., and Silliman, B.R. (2005). Linking biogeography and community ecology: latitudinal variation in plant-herbivore strength. Ecology *86*, 2310–2319.

110. Pennings, S.C., Ho, C.-K., Salgado, C.S., Wieski, K., Davé, N., Kunza, A.E., and Wason, E.L. (2009). Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. Ecology *90*, 183–195.

111. He, Q., and Silliman, B.R. (2015). Biogeographic consequences of nutrient enrichment for plant–herbivore interactions in coastal wetlands. Ecol. Lett. *18*, 462–471. https://doi.org/10.1111/ele.12429.

112. Juan-Baeza, I., Martínez-Garza, C., and del-Val, E. (2015). Recovering more than tree cover: Herbivores and herbivory in a restored tropical dry forest. PLoS One *10*, 128583. https://doi.org/10.1371/journal.pone.0128583.

113. Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., and West, G.B. (2004). Toward a metabolic theory of ecology. Ecology *85*, 1771–1789. https://doi.org/10.1890/03-9000.

114. Enquist, B.J., Economo, E.P., Huxman, T.E., Allen, A.P., Ignace, D.D., and Gillooly, J.F. (2003). Scaling metabolism from organisms to ecosystems. Nature *423*, 639–642. https://doi.org/10.1038/nature01671.

115. López-Urrutia, Á., San Martin, E., Harris, R.P., and Irigoien, X. (2006). Scaling the metabolic balance of the oceans. Proc. Natl. Acad. Sci. USA *103*, 8739–8744. https://doi.org/10.1073/pnas.0601137103.

116. Makarieva, A.M., Gorshkov, V.G., Li, B.-L., Chown, S.L., Reich, P.B., and Gavrilov, V.M. (2008). Mean mass-specific metabolic rates are strikingly similar across life's major domains: Evidence for life's metabolic optimum. Proc. Natl. Acad. Sci. USA *105*, 16994–16999. https://doi.org/10.1073/pnas.0802148105.

117. Huey, R.B., and Kingsolver, J.G. (2019). Climate warming, resource availability, and the metabolic meltdown of ectotherms. Am. Nat. *194*, 140–150. https://doi.org/10.1086/705679.

118. Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Zeller, D., and Pauly, D. (2010). Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Glob. Change Biol. *16*, 24–35. https://doi.org/10.1111/j.1365-2486.2009.01995.x.

119. Cheung, W.W.L., Watson, R., and Pauly, D. (2013). Signature of ocean warming in global fisheries catch. Nature *497*, 365–368. https://doi.org/10.1038/nature12156.

120. Fyllas, N.M., Bentley, L.P., Shenkin, A., Asner, G.P., Atkin, O.K., Díaz, S., Enquist, B.J., Farfan-Rios, W., Gloor, E., and Guerrieri, R. (2017). Solar radiation and functional traits explain the decline of forest primary productivity along a tropical elevation gradient. Ecol. Lett. *20*, 730–740. https://doi.org/10.1111/ele.12771.

121. Wieczynski, D.J., Díaz, S., Durán, S.M., Fyllas, N.M., Salinas, N., Martin, R.E., Shenkin, A., Silman, M.R., Asner, G.P., and Bentley, L.P. (2022). Improving landscape-scale productivity estimates by integrating trait-based models and remotely-sensed foliar-trait and canopy-structural data. Ecography 6078. https://doi.org/10.1111/06078.

122. Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., Sloat, L.L., and Savage, V.M. (2015). Scaling from traits to ecosystems. Adv. Ecol. Res. *52*, 249–318. https://doi.org/10.1016/bs.aecr.2015.02.001.

123. Galbraith, E., Frade, P.R., and Convertino, M. (2022). Metabolic shifts of oceans: Summoning bacterial interactions. Ecol. Indic. *138*, 108871. https://doi.org/10.1016/j.ecolind.2022.108871.

124. Wieczynski, D.J., Singla, P., Doan, A., Singleton, A., Han, Z.-Y., Votzke, S., Yammine, A., and Gibert, J.P. (2021). Linking species traits and demography to explain complex temperature responses across levels of organization. Proc. Natl. Acad. Sci. USA *118*, e2104863118. https://doi.org/10.1073/pnas.2104863118.

125. Schuwirth, N., and Reichert, P. (2013). Bridging the gap between theoretical ecology and real ecosystems: modeling invertebrate community composition in streams. Ecology *94*, 368–379. https://doi.org/10.1890/12-0591.1.

126. Woodward, G., Ebenman, B., Emmerson, M., Montoya, J., Olesen, J., Valido, A., and Warren, P. (2005). Body size in ecological networks. Trends Ecol. Evol. *20*, 402–409. https://doi.org/10.1016/j.tree.2005.04.005.

127. Clarke, A. (2006). Temperature and the metabolic theory of ecology. Funct. Ecol. *20*, 405–412. https://doi.org/10.1111/j.1365-2435.2006.01109.x.

128. Fulton, E.A., Blanchard, J.L., Melbourne-Thomas, J., Plagányi, É.E., and Tulloch, V.J.D. (2019). Where the ecological gaps remain, a modelers' perspective. Front. Ecol. Evol. *7*, 424. https://doi.org/10.3389/fevo.2019.00424.

129. de Ruiter, P.C., Neutel, A.-M., and Moore, J.C. (1995). Energetics, patterns of interaction strengths, and stability in real ecosystems. Science *269*, 1257–1260. https://doi.org/10.1126/science.269.5228.1257.

130. Klausmeier, C.A. (1999). Regular and irregular patterns in semiarid vegetation. Science *284*, 1826–1828. https://doi.org/10.1126/science.284.5421.1826.

131. Rietkerk, M., and Van De Koppel, J. (2008). Regular pattern formation in real ecosystems. Trends Ecol. Evol. *23*, 169–175. https://doi.org/10.1016/j.tree.2007.10.013.

132. de Paoli, H., Van Der Heide, T., Berg, A., Silliman, B.R., Herman, P.M.J., and Van De Koppel, J. (2017). Behavioral self-organization underlies the resilience of a coastal ecosystem. Proc. Natl. Acad. Sci. USA *114*, 8035–8040. https://doi.org/10.1073/pnas.1619203114.

133. Berghuis, P.M.J., Mayor, Á.G., Rietkerk, M., and Baudena, M. (2020). More is not necessarily better: The role of cover and spatial organization of resource sinks in the restoration of patchy drylands. J. Arid Environ. *183*, 104282. https://doi.org/10.1016/j.jaridenv.2020.104282.

134. Rietkerk, M., Boerlijst, M.C., Langevelde, F., HilleRisLambers, R., van Koppel, J., Kumar, L., Prins, H.H.T., and Roos, A.M. (2002). Self-organization of vegetation in arid ecosystems. Am. Nat. *160*, 524–530. https://doi.org/10.1086/342078.

135. Tilman, D., Isbell, F., and Cowles, J.M. (2014). Biodiversity and ecosystem functioning. Annu. Rev. Ecol. Evol. Syst. *45*, 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917.

136. Raffard, A., Santoul, F., Cucherousset, J., and Blanchet, S. (2019). The community and ecosystem consequences of intraspecific diversity: a meta-analysis. Biol. Rev. *94*, 648–661. https://doi.org/10.1111/brv.12472.

137. Laughlin, D.C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecol. Lett. *17*, 771–784. https://doi.org/10.1111/ele.12288.

138. Carlucci, M.B., Brancalion, P.H.S., Rodrigues, R.R., Loyola, R., and Cianciaruso, M.V. (2020). Functional traits and ecosystem services in ecological restoration. Restor. Ecol. *28*, 1372–1383. https://doi.org/10.1111/rec.13279.

139. Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., and Jouseau, C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature *443*, 989–992. https://doi.org/10.1038/nature05202.

140. Loreau, M., Mouquet, N., and Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. Proc. Natl. Acad. Sci. USA *100*, 12765–12770. https://doi.org/10.1073/pnas.2235465100.

141. Yachi, S., and Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc. Natl. Acad. Sci. USA *96*, 1463–1468. https://doi.org/10.1073/pnas.96.4.1463.

142. Isbell, F., Cowles, J., Dee, L.E., Loreau, M., Reich, P.B., Gonzalez, A., Hector, A., and Schmid, B. (2018). Quantifying effects of biodiversity on ecosystem functioning across times and places. Ecol. Lett. *21*, 763–778. https://doi.org/10.1111/ele.12928.

143. Wilsey, B. (2021). Restoration in the face of changing climate: importance of persistence, priority effects, and species diversity. Restor. Ecol. *29*, e13132. https://doi.org/10.1111/rec.13132.

144. Williams, S.L., Ambo-Rappe, R., Sur, C., Abbott, J.M., and Limbong, S.R. (2017). Species richness accelerates marine ecosystem restoration in the Coral Triangle. Proc. Natl. Acad. Sci. USA *114*, 11986–11991. https://doi.org/10.1073/pnas.1707962114.

145. Schmitz, O.J., Sylvén, M., Atwood, T.B., Bakker, E.S., Berzaghi, F., Brodie, J.F., Cromsigt, J.P.G.M., Davies, A.B., Leroux, S.J., Schepers, F.J., *et al*. (2023). Trophic rewilding can expand natural climate solutions. Nat. Clim. Chang. *13*, 324–333. https://doi.org/10.1038/s41558-023-01631-6.

146. Bellwood, D.R., Hoey, A.S., Ackerman, J.L., and Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Glob. Chang. Biol. *12*, 1587–1594. https://doi.org/10.1111/j.1365-2486.2006.01204.x.

147. Hensel, M.J.S., Patrick, C.J., Orth, R.J., Wilcox, D.J., Dennison, W.C., Gurbisz, C., Hannam, M.P., Landry, J.B., Moore, K.A., Murphy, R.R., *et al*. (2023). Rise of *Ruppia* in Chesapeake Bay: Climate change–driven turnover of foundation species creates new threats and management opportunities. Proc. Natl. Acad. Sci. USA *120,* e2220678120. https://doi.org/10.1073/pnas.2220678120.

148. Hensel, E., Patrick, C.J., Wilson, S.J., Song, B., Reay, W., and Orth, R.J. (2024). Incorporating generalist seagrasses enhances habitat restoration in a changing environment. J. Appl. Ecol. https://doi.org/10.1111/1365–266414643.

149. Orth, R.J., Lefcheck, J.S., McGlathery, K.S., Aoki, L., Luckenbach, M.W., Moore, K.A., Oreska, M.P.J., Snyder, R., Wilcox, D.J., and Lusk, B. (2020). Restoration of seagrass habitat leads to rapid recovery of coastal ecosystem services. Sci. Adv. *6*, eabc6434. https://doi.org/10.1126/sciadv.abc6434.

150. Valdez, S.R., Zhang, Y.S., Van Der Heide, T., Vanderklift, M.A., Tarquinio, F., Orth, R.J., and Silliman, B.R. (2020). Positive ecological interactions and the success of seagrass restoration. Front. Mar. Sci. *7*, 91. https://doi.org/10.3389/fmars.2020.00091.

151. Harris, J.A., Hobbs, R.J., Higgs, E., and Aronson, J. (2006). Ecological Restoration and global climate change. Restor. Ecol. *14*, 170–176. https://doi.org/10.1111/j.1526-100X.2006.00136.x.

152. Rice, K.J., and Emery, N.C. (2003). Managing microevolution: Restoration in the face of global change. Front. Ecol. Environ. *1*, 469–478. https://doi.org/10.1890/1540-9295(2003)001.

153. Futuyma, D., and Kirkpatrick, A.M. (2017). Evolution, 4th edn. (Oxford: Oxford University Press).

154. McKay, J.K., Christian, C.E., Harrison, S., and Rice, K.J. (2005). How local is local A review of practical and conceptual issues in the genetics of restoration. Restor. Ecol. *13*, 432–440. https://doi.org/10.1111/j.1526-100X.2005.00058.x.

155. Leibold, M.A. (2018). Metacommunity Ecology (Princeton, NJ: Princeton University Press).

156. Hartl, D.L., and Clark, A.G. (2007). Principles of Population Genetics, 4th ed. (Sunderland, MA: Sinauer Associates).

157. Camazine, S. (2003). Self-organization in Biological Systems (Princeton, NJ: Princeton University Press).

158. Sibly, R.M., Brown, J.H., and Kodric-Brown, A. (2012). Metabolic Ecology: A Scaling Approach (Oxford: Wiley-Blackwell).

159. McCann, K.S. (2012). Food Webs (Princeton, NJ: Princeton University Press).

160. Hale, R., and Swearer, S.E. (2017). When good animals love bad restored habitats: How maladaptive habitat selection can constrain restoration. J. Appl. Ecol. *54*, 1478–1486. https://doi.org/10.1111/1365-2664.12829.

161. Maschinski, J., and Quintana-Ascencio, P.F. (2016). Implications of population and metapopulation theory for restoration science and practice. In Foundations of Restoration Ecology, M.A. Palmer, J.B. Zedler, and D.A. Falk, eds. (Washington DC: Island Press), pp. 182–215. https://doi.org/10.5822/978-1-61091-698-1_7.

162. Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B., and Charnov, E.L. (2004). Effects of body size and temperature on population growth. Am. Nat. *163*, 429–441. https://doi.org/10.1086/381872.

163. Zhao, L.-X., Xu, C., Ge, Z.-M., Koppel, J., and Liu, Q.-X. (2019). The shaping role of self-organization: Linking vegetation patterning, plant traits and ecosystem functioning. Proc. R. Soc. Lond. B Biol. Sci. *286*, 20182859. https://doi.org/10.1098/rspb.2018.2859.

164. MacArthur, R.H., and Wilson, E.O. (2001). The Theory of Island Biogeography (Princeton, NJ:: Princeton University Press).

165. Reznick, D., Bryant, M.J., and Bashey, F. (2002). r- and K-selection revisited: the role of population regulation in life-history evolution. Ecology *83*, 1509–1520. https://doi.org/10.1890/0012-9658(2002)083.

166. Vander Zanden, M.J., Olden, J.D., Gratton, C., and Tunney, T.D. (2016). Food web theory and ecological restoration. In Foundations of Restoration Ecology, M.A. Palmer, J.B. Zedler, and D.A. Falk, eds. (Washington DC: Island Press), pp. 301–329. https://doi.org/10.5822/978-1-61091-698-1_11.

167. Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., and Baraza, E. (2004). Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. Ecol. Appl. *14*, 1128–1138. https://doi.org/10.1890/03-5084.

168. Holyoak, M., Leibold, M.A., and Holt, R.D. (2005). Metacommunities: Spatial Dynamics and Ecological Communities (Chicago: University of Chicago Press).

169. Hubbell, S.P. (2001). The Unified Neutral Theory of Biodiversity and Biogeography (Princeton, NJ: Princeton University Press).

170. Palik, B.J., Goebel, P.C., Kirkman, L.K., and West, L. (2000). Using landscape hierarchies to guide restoration of disturbed ecosystems. Ecol. Appl. *10*, 189–202. https://doi.org/10.1890/1051-0761(2000)010.

171. Gunderson, L.H. (2000). Ecological resilience—in theory and application. Annu. Rev. Ecol. Syst. *31*, 425–439.

172. Solé, R.V., and Bascompte, J. (2006). Self-Organization in Complex Ecosystems (Princeton, NJ: Princeton University Press). https://doi.org/10.1515/9781400842933.

173. Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343.

174. Estes, J., Crooks, K., and Holt, R.D. (2013). Ecological role of predators. Encyclopedia of Biodiversity, 2nd edn. *4*, 229–249. https://doi.org/10.1016/B978-0-12-384719-5.00117-9.

175. Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., and Vasseur, D.A. (2011). Why intraspecific trait variation matters in community ecology. Trends Ecol. Evol. *26*, 183–192. https://doi.org/10.1016/j.tree.2011.01.009.

176. Schramski, J.R., Dell, A.I., Grady, J.M., Sibly, R.M., and Brown, J.H. (2015). Metabolic theory predicts whole-ecosystem properties. Proc. Natl. Acad. Sci. USA *112*, 2617–2622. https://doi.org/10.1073/pnas.1423502112.

177. Montoya, D., Rogers, L., and Memmott, J. (2012). Emerging perspectives in the restoration of biodiversity-based ecosystem services. Trends Ecol. Evol. *27*, 666–672. https://doi.org/10.1016/j.tree.2012.07.004.

178. Ritchie, E.G., and Johnson, C.N. (2009). Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett. *12*, 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x.

179. Levin, S.A. (1998). Ecosystems and the biosphere as complex adaptive systems. Ecosystems *1*, 431–436. https://doi.org/10.1007/s100219900037.