Restoration through reassembly: plant traits and invasion resistance

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One of the greatest challenges for ecological restoration is to create or reassemble plant communities that are resistant to invasion by exotic species. We examine how concepts pertaining to the assembly of plant communities can be used to strengthen resistance to invasion in restored communities. Community ecology theory predicts that an invasive species will be unlikely to establish if there is a species with similar traits present in the resident community or if available niches are filled. Therefore, successful restoration efforts should select native species with traits similar to likely invaders and include a diversity of functional traits. The success of trait-based approaches to restoration will depend largely on the diversity of invaders, on the strength of environmental factors and on dispersal dynamics of invasive and native species.

Trait-based community assembly as a framework for the restoration of invaded systems

As ecosystems worldwide are degraded by human activity, ecological restoration plays an essential role in maintaining biodiversity and critical ecosystem functions. The invasion of exotic species poses a special challenge to ecosystem restoration, as invaders often both contribute substantially to ecosystem degradation and hinder efforts to restore systems [1]. An essential component of restoration is the reassembly of plant and animal communities following ecosystem degradation or the removal of invasive species. Especially for completely denuded sites, designing communities that can resist invasion by exotic species is often a primary goal. In this review, we focus on invasion-resistant restoration starting from bare ground, but note that many of the same principles will apply to efforts aimed at improving the quality of communities starting from intermediate points (e.g. a mixed native and exotic community).

The utility of scientific theory in restoration efforts has been the topic of recent debate [2,3]. Trial-and-error approaches that are not based on scientific theory can be effective but are largely applicable to specific systems or species [3]. For example, many attempts to restore invaded systems have failed, in part owing to the lack of a community-oriented integrated framework [4]. Without an understanding of plant species resource use, dispersal and stress tolerance, current restoration methods such as invasive species removal, fertilization or fire could favor existing invasive species or promote further invasion [5].

Many recent developments in community ecology are significantly advancing our understanding of restoration in invaded systems [6–8]. In this review, we build on earlier efforts that have applied community ecology theory to mechanisms of biological invasion [9–13] to explore how a trait-based community framework can guide restoration efforts to assemble plant communities that are resistant to invasion. Specifically, we highlight recent evidence that the selection of native species based on resource-use traits will increase community resistance to invasion, and predict the success of habitat manipulations (e.g. fire, mowing) for restoration.

Community ecology theory

For decades, ecologists have debated whether communities assemble following a set of nonrandom rules [14–17]. Much recent debate has focused on whether community assembly is more strongly limited by the availability of environmentally suitable sites (niche limitation) or the likelihood of plant species reaching those sites (dispersal limitation) [18–21]. A more integrated view of community assembly separates niche and dispersal limitation into individual ecological filters, where species from a regional pool are ‘filtered out’ of the local community by various dispersal, biotic and

Glossary

Competitive exclusion: two species competing for the same resources cannot stably coexist, if the ecological factors are constant.
Complementarity: two or more species use resources in complementary ways such that together they more effectively use available resources than either does alone [7].
Ecological filter: dispersal, environmental or biotic factors that limit which species are present in a community.
Ecological restoration: the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed.
Effect traits: traits that influence ecosystem processes such as primary productivity, nutrient cycling and trophic transfer [68,69].
Functional redundancy: two or more species are substitutable with respect to their contributions to a single ecosystem function [7].
Functional traits: the ecological attributes of a species that relate both to strategies of resource capture and to the effect of that species on the overall pool of resources in the ecosystem [29].
Limiting similarity: there is a finite limit to the similarity in resource use between coexisting species [28].
Phenotypic plasticity: broadly defined as the ability of organisms to alter behavioral, morphological and/or physiological traits in response to varying environmental conditions.
Response traits: traits that describe species response to biotic and abiotic factors such as resource availability, disturbance and herbivory pressure [69].

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Box 1. Scale dependence: the role of ecological filters

Functional traits are not only a reflection of species resource capture strategies, they also reflect strategies for reproduction and dispersal, and are related to environmental tolerances (Figure I). Processes acting at different scales to influence the process of community assembly can be seen as a series of 'filters' [22,23]. At the largest scale, dispersal traits can determine which invasive species are present in the species pool, such that invasive species might possess traits specifically related to long-distance dispersal, which native species might or might not also have. Environmental conditions constrain the traits of species which can persist in a region, which would tend to result in trait similarities between native and invasive species at a site. Finally, it is only at the small scale of the local neighborhood that individuals compete, and we would expect to see trait differences between native and invasive species as a result of limiting similarity. Restoration can act on each of these filters to influence community composition [23]. For instance, dispersal filters can be overcome by planting, environmental filters can be modified by ecosystem-based management practices such as controlled burns, and biotic interactions can be influenced by maintaining appropriate levels of herbivory, adding important mycorrhizal associates, or selecting native species with highly competitive traits (e.g. high water-use efficiency in arid systems or fast growth rate in a shaded forest understory). Restoration favoring native species with particular suites of traits would then ideally allow the community to resist invasion by functionally similar invasive species.

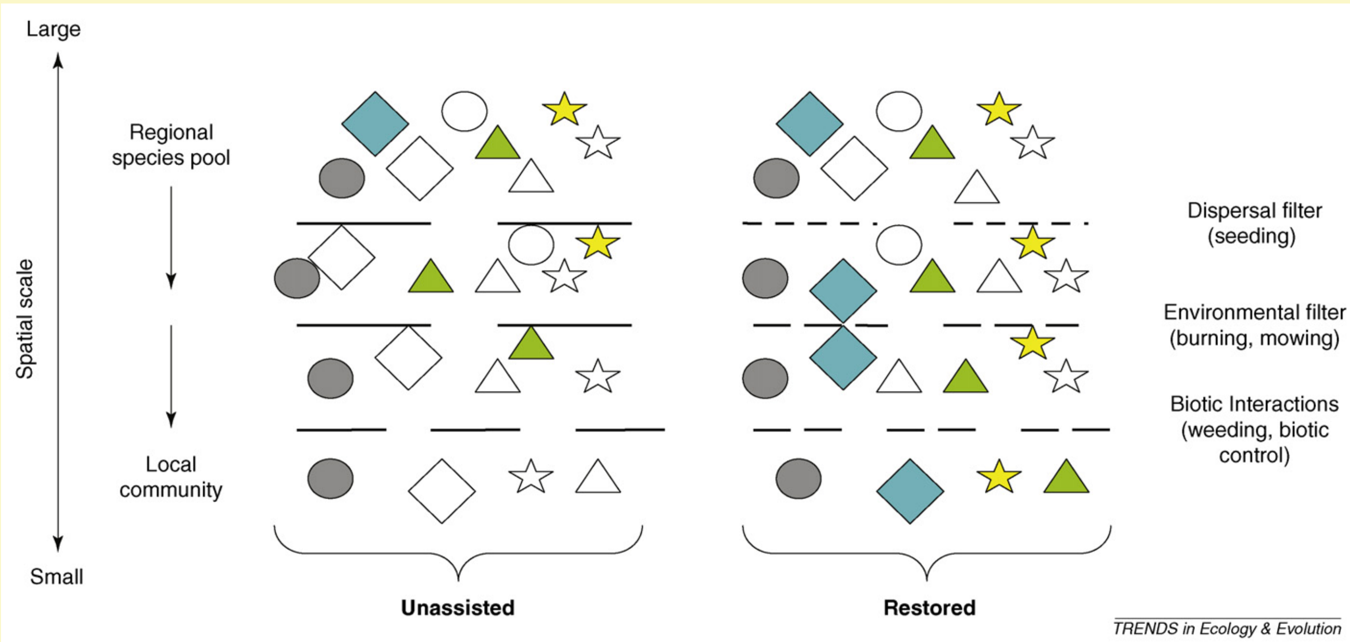

Figure I. Ecological filters act at multiple spatial scales to determine community composition (axis left). By influencing filters, restoration can guide community assembly (restoration strategies shown in parentheses on the right of the figure). Similar species are indicated using the same symbol; in each case, native species are shown in closed colored symbols and invasive species are in open white symbols.

environmental mechanisms [22,23]. Dispersal, biotic and environmental filters determine which functional traits or trait values will be optimal for a particular environment (Box 1). These filters will thereby limit the range of viable ecological strategies in a community and will lead to various distributions of traits within the community.

Environmental and biotic filters represent opposing forces in terms of assembly, and the relative strength of each filter will determine which species are likely to invade. Environmental filters will cause species that are closer to the environmental optimum, and more similar to other species, to be more abundant or more likely to invade, which will generate trait clumping (underdispersion; species are more similar than expected by chance). Conversely, competitive exclusion, a primary biotic filter, should limit the trait similarity of co-occurring species and generate trait evenness (or overdispersion; species are less similar than expected by chance) [24,25]. This outcome is termed niche limitation or limiting similarity. An extension of these ideas, that niche space saturates as a community contains more species, has also formed the basis of the hypothesis that species richness confers invasion resistance [26,27]. Through more efficient resource capture, a functionally diverse native community can eliminate or reduce vacant niches available to invaders.

As an example of these opposing forces, low water availability is a strong environmental filter that decreases the breadth of plant traits (closer to the environmental optimum) in a community, but causes more intense competition for the limiting resource because species are more similar with respect to key traits (e.g. water-use efficiency; Box 2). The existence of empty niche space in these systems will determine whether a species can invade and, if so, the abundance it can achieve [28]. Thus, communities containing native species that are functionally similar to invasive species with respect to these traits should be the most resistant to invasion.

The trait-based community framework suggests at least three ways that restoration could limit exotic species invasion. First, limiting similarity theory predicts that successful invaders will differ functionally from species already present in the community, and that successful restoration approaches would be ones that build native communities with traits similar to potential invaders. Second, invasion

Box 2. Evaluating functional traits

Multivariate analysis of functional traits can be used to select native plant communities that are likely to resist invasion. Figure Ia shows the trait space for multiple invasive and native species sampled from dry forests in Hawai'i. Many native species show trait space overlap with invasive species for key resource-use traits, and limiting similarity theory suggests that these native species will be most able to compete with invaders in this habitat and, thus, be good candidates for restoration projects.

One invasive species (*Leucaena leucocephala*; red circle in Figure Ia) is functionally distinct from all other species. According to the limiting similarity framework, this species would be most likely to invade. However, it is outside the environmental filter, which suggests that it might not succeed. *L. leucocephala* is a nitrogen-fixing shrub that was introduced as cattle feed on several Hawaiian Islands. It produces copious amounts of seed and might persist in this system (outside of the environmental filter) by relying on seed banks during unfavorable (i.e. dry) years or seasons or on dispersal by ungulates to more favorable habitats.

Trait space overlap will change as environmental filters are narrowed and widened. Drier conditions associated with climate change projections could further restrict the number of species in this community (narrowed environmental filter). In dry forests, species with low water-use efficiency and thin, nutrient-rich leaves are not likely to persist (Figure Ib). This reduces the trait space overlap between native and invasive species, but eliminates many invasive species from the system.

Conversely, nitrogen deposition could act to broaden the environmental filter and allow more species to invade (Figure Ic). In addition, the trait space of natives and invaders could change if plant species respond to environmental change with phenotypic plasticity. In our example, invasive species demonstrate physiological plasticity in response to the added N, depicted by movement in trait space toward higher leaf nitrogen and photosynthetic rates (thin arrows). (Figure Ic). Plasticity by invaders reduces the trait space overlap with native species.

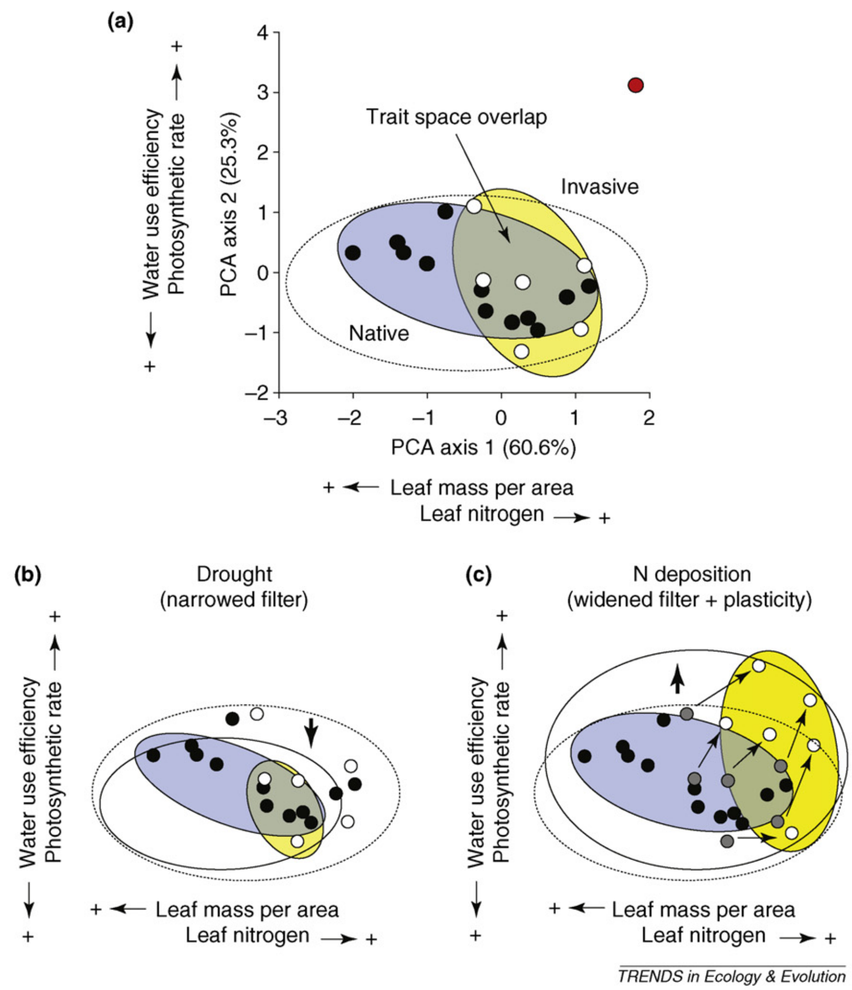

Figure I. Multivariate analysis of functional trait data. **(a)** Seven invasive (white circles, yellow ellipse) and 12 native species (black circles, blue ellipse) were sampled from dry forests in Hawai'i [32,81,82]. The dotted ellipse represents the initial ecological filter in each panel. Four leaf-level traits pertaining to resource use were selected. One invasive species is functionally distinct from all other species (red circle). **(b)** Drought hypothetically narrows the environmental filter which reduces the number of individuals that will survive in that habitat (solid ellipse, thick arrow). **(c)** Nitrogen deposition hypothetically widens the environmental filter (solid ellipse, thick arrow), potentially allowing more individuals to exist in the habitat. In this example, invasive species respond plastically to increased nutrient availability whereas natives do not (thin arrows).

would be predicted to occur if an ecological filter changes (for instance, owing to human transport of seed or resource enhancement), thereby expanding or shifting the potential trait breadth of the community. Restoration efforts should therefore integrate likely changes in ecological filters into the process of community design. Last, native communities might be vulnerable to invasion if their traits are not well dispersed over available niche space, which would leave available resources for a new species to establish. Thus, increasing the functional diversity of the native plant community might increase invasion resistance. In the following sections, we expand on each of these three ideas and include recent evidence and suggestions for restoration practitioners. Because all of these predictions depend on understanding functional differences among species, we first review how to select and measure relevant functional traits for restoration projects.

Identifying relevant functional traits

Perhaps the biggest challenge in applying functional traits to restoration design is deciding which functional traits are relevant and measurable for a given habitat. Functional traits are typically classified as response or effect traits [29,30], but these designations are not mutually exclusive. The functional significance of various traits to plant fitness (response) and ecosystem processes (effect) are presented in Table 1.

When selecting species for a restoration project, the relative importance of response and effect traits will depend on the objectives and challenges of the project. Some of the most problematic invasive species are those that invade and change ecosystem function [31]. This occurs because native and invasive species often have different effect traits. If the goal of restoration is to maintain ecosystem function, and response traits of the invader enable invasion, then the best native species for restoration might be those that share response traits with the invader (limiting similarity) but have different effect traits. For example, exotic grasses and native woody species in arid systems could have similar water-use traits [32] but different effect traits, as grasses are highly flammable during the dry season, and thus might increase the vulnerability of the system to wildfires [33].

The most relevant functional traits can be difficult to measure, especially for multiple species within a community. For example, growth and physiology measures are time consuming and/or require expensive equipment. However, several easy-to-measure traits are often correlated with key processes [34]. For example, many physiological (photosynthetic rate), morphological (leaf mass per area) and reproductive (seed size) traits are representative of species differences in light acquisition and shade tolerance [35–38]. Leaf mass per unit area is a key predictor of plant ecological strategies [39] and can be used to estimate growth rate, stress tolerance and leaf longevity. Such traits can thus be used as a proxy for the relevant functional traits, reducing the need for more difficult measurements.

In applying functional traits to restoration efforts, a practitioner should also consider the influence of phylogenetic history. Because recently diverged species tend to have similar functional traits [40], the evolutionary relatedness of organisms in a community will affect the traits of the community as well as the processes that determine invasion resistance. Trait similarity among related taxa suggests that phylogeny could be used as a proxy for trait similarity if functional traits cannot be determined (i.e. choose native species that are closely related to the invasive species). However, several studies have found that differences in a few key traits between closely related species can promote invasiveness [32,41], suggesting that this approach might not work in all communities. For example, an examination of morphological and performance traits of five congeneric pairs of invasive and noninvasive species in spiderworts (Commelinaceae) found that the invasive species had greater sexual and vegetative reproduction, higher specific leaf area and greater relative growth rates than noninvasive congeners [41]. Thus, although taxonomic relatedness might be a good first cut in assessing functional traits, we recommend using measurements or published trait values (e.g. USDA TRAIT database, http://www.plants.usda.gov) to further evaluate functional traits.

Applying the concept of limiting similarity to ecological restoration

The concept of limiting similarity predicts that invasive species will be unlikely to establish if there are native species with similar traits present in the resident community or if available niches are filled. Several plot-scale and mesocosm studies suggest that limiting similarity does indeed confer invasion resistance [42–45] (but see Ref. [46]). In a European grassland, the invasion of exotic legumes was low in native legume communities relative to communities composed of native grasses and nonleguminous forbs [45]. In a California annual grassland, an invasive starthistle (*Centaurea solstitialis*) had lower biomass in communities containing the functionally similar tarweed (*Hemizonia congesta*) [42]; both species are late-active annual forbs and compete for late-season soil moisture. A seeding experiment in a Minnesota prairie grassland found that species were least likely to invade when there was a functionally similar species present [44]. Finally, in an oldfield and in grassland mesocosms, a

Table 1. Traits can simultaneously influence species *response* to environmental and biotic factors and the *effect* of species on ecosystem processes [34,68,69]; however, response and effect traits need not be correlated with one another [29]

Trait	Response	Effect
Leaf mass per area	Growth, palatability, competitive ability, leaf longevity	Primary productivity
Leaf weight ratio	Growth	Primary productivity
Plant height	Competitive ability	Primary productivity, microclimate
Leaf nitrogen content	Growth, palatability, decomposability	Primary productivity, trophic transfer[a], nutrient cycling
Seed mass	Dispersal distance, establishment success	Trophic transfer
Phenology	Competitive ability	Nutrient cycling, microclimate, trophic transfer
Resource-use efficiency	Competitive ability, stress tolerance	Primary productivity, resource availability
Litter quality	Stress tolerance	Fire frequency
Soil biota associations	Growth, stress tolerance	Nutrient cycling

[a]Trophic transfer refers to energy transfer across trophic levels through herbivory and frugivory.

Box 3. When is the concept of limiting similarity the most likely to benefit restoration?

Many hypotheses have been proposed to explain the success of invasive species in their new habitats, and different restoration strategies are appropriate depending on the dominant mechanism promoting invasion (see Table I). Restoration strategies are most likely to benefit from incorporating the concept of limiting similarity in cases where planting or seeding is planned, such as on denuded landscapes. In these areas, restoration practitioners are choosing the composition of the native community, and they have the opportunity to pick native species that are likely to compete with and exclude exotic species that could subsequently invade from surrounding areas. This choice should represent a merging of local natural history knowledge with general ecological concepts. Whereas restoration texts often focus on the need to choose species that are adapted to the environmental conditions, or to include many 'functional groups' to increase the chance of having good native competitors, there has not yet been a push to choose native species that are ecologically similar to problematic invaders (e.g. [83]). For instance, in California grasslands, many exotic species are active early in the growing season [84]. By incorporating early-active native species in plantings, practitioners might be able to reduce the degree to which exotic species are able to invade newly restored areas. Roadsides are another case where the concept of limiting similarity could benefit restoration. Roadsides have high seed rain from external areas and are often invaded by 'weedy' exotic species [85]. Experimental evidence suggests that many native plant populations are seed limited, so simply seeding native species into these areas could help reduce exotic species success [47]. The concept of limiting similarity would predict that similarly 'weedy' natives would do well on roadsides, namely native species with high growth rates that tend to be found in disturbed areas and have high nutrient requirements.

Table I. When limiting similarity will not work: alternative mechanisms of invasion and proposed restoration strategies

Hypothesized factors that promote invasion	Restoration strategy to counteract the invasive species advantage
Release from natural enemies [77]	Biocontrol, controlled grazing
High resource availability [64]	Mowing, carbon additions to lower soil nitrogen availability, planting canopy trees to lower light availability
High resource-use efficiency [32]	Fire or targeted herbicide, weeding to remove exotics
Beneficial associations, invasional meltdown [78]	Maintain native mutualisms, add native mycorrhizal inoculates to soil
Empty niche, lack of competition [9]	Planting or seeding native species to increase biotic resistance
Altered disturbance regimes [79]	Return to traditional fire or flood regime
High propagule pressure [80]	Seeding natives to counteract high seed rain of exotics

seeding experiment found that both native and nonnative species were more likely to establish when a functionally similar species was absent [43]. However, statistically significant patterns were only found for one-third of the seeded species, suggesting that other mechanisms also predicted invader success.

Differences in the timing and pattern of resource use represent just one of the many mechanisms by which species invade (Box 3). For example, several studies in invaded systems have found that community dynamics are more strongly influenced by dispersal filters than resource-use traits associated with limiting similarity [47,48]. In a California grassland, low water availability acted as a strong environmental filter for an invasive perennial grass; however, once this environmental filter was overcome (by water addition), seed density most strongly influenced the likelihood of invasion [49]. Thus, eliminating the seed banks (e.g. by removing topsoil and by repeated mowing to reduce seed input) and reducing the dispersal of invasive species into restored communities (e.g. managing populations of rodent and ungulate dispersers, removing adjacent invaders) might be the most effective restoration strategies in systems where native species suffer recruitment limitation.

Incorporating ecological filters into the design of restored communities

Ecological filters influence community assembly at multiple scales (Box 1). Evaluating the trait space of native and invasive species within a community might suggest methods to alter ecological filters to prevent invasion in restored communities. This evaluation could be particularly important where limiting similarity will not work, as when there are no native species in the regional species pool that are functionally similar to invaders (e.g. no suitable natives share resource-use traits with invaders). When limiting similarity is not a valid restoration strategy, manipulating ecological filters, such as resource availability, might successfully favor the growth of native species. Several studies suggest that lowering soil nitrogen [50,51] and phosphorus [52] availability will decrease the growth of nutrient-demanding invasive species. Reducing light availability by planting or seeding canopy species can curtail the growth of shade-intolerant invasive species or provide more favorable microhabitats for native species [53,54]. In other cases, restoration efforts could be enhanced by restoring or eliminating disturbance regimes, for example with mowing or fire [55].

Whereas many of these filter manipulations reflect commonsense approaches that restoration practitioners regularly use [2], we propose that the success of these manipulations can be predicted *a priori* by examining the distribution of relevant traits (e.g. resource use or flammability) for invasive and native species. For filter manipulations to work, invasive and native species must occupy different trait space with respect to limiting resources and disturbance regimes [32]. For example, invasive grasses can be effectively controlled by planting canopy species to lower light availability [53,54] because invasive grasses and native woody species differ in shade tolerance traits. Shade-tolerant woody species generally possess a suite of physiological traits to maximize light capture such as high chlorophyll content and allocation of nitrogen to proteins associated with light harvesting functions at the expense of carbon assimilation functions [36,56]. Shade-tolerant species also have high leaf mass per area, leaf longevity (which increases the lifetime carbon assimilation of the leaf) and seed mass [38,39]. Examining these traits for all relevant native and invasive species before a manipulation (as in Box 2) will inform a practitioner about the potential success of such a restoration strategy.

When manipulating ecological filters based on functional traits, it is important to consider how plant size and age influence trait values and the association between traits and plant fitness [37]. For example, adult individuals of native and invasive species in Hawaiian dry forests have similar water-use traits (Box 2), which suggests that altering water availability (by tarping or adding supplemental water) might not influence native species success in these systems. However, a water addition study conducted on seedlings in these Hawaiian dry forests contradicted this prediction [57]. The authors found that native seedlings responded more positively to water addition than did invasive seedlings. This illustrates an important discrepancy between which functional trait data are collected and which functional trait data actually determine competitive outcomes. Most functional traits are measured on adult individuals, whereas seedlings are the most vulnerable to environmental stress, competition and herbivory [58]. Thus, the functional traits of seedlings could tell us more about the potential distribution and patterns of competition and coexistence of species [4].

Ecological filters and environmental change

Whereas restoration ecology has largely focused on returning systems to a historical state, there is a growing consensus that restoration efforts must plan for future environmental conditions [59,60]. Environmental change could constrict or broaden ecological filters within communities (Box 2). Species response traits can be valuable tools for restoration planning if future environmental conditions can be predicted. For example, selecting drought- or stress-tolerant species could help mediate community response to forecasted aridity in the southwestern United States or increased disturbance due to flooding along coastlines in many parts of the world [61]. Additionally, including functional redundancy for important environmental responses or ecosystem functions will ensure that some individuals within a restored community survive environmental perturbation (Figure 1).

Numerous studies have found that invasive species are more phenotypically plastic than native species (e.g. [62,63]) and differences in phenotypic plasticity among native and invasive species will influence how restored communities will respond to altered environmental conditions associated with climate change or deliberate manipulations of abiotic filters for the purpose of restoration. In a hypothetical example, invasive species might be better able than native species to respond to increased nutrient availability (resulting from agricultural runoff or atmospheric deposition [64]) by increasing nutrient uptake, leaf nitrogen content, photosynthetic rate and biomass (Box 2). These responses will provide an advantage for invasive species over native species, complicating restoration efforts. Differential plastic responses among species can also reduce trait space overlap and the likelihood that limiting similarity approaches will work in restored systems. Because plant species display various degrees of phenotypic plasticity in response to environmental change, functional traits need to be measured across a range of expected environments to anticipate potential changes in trait space.

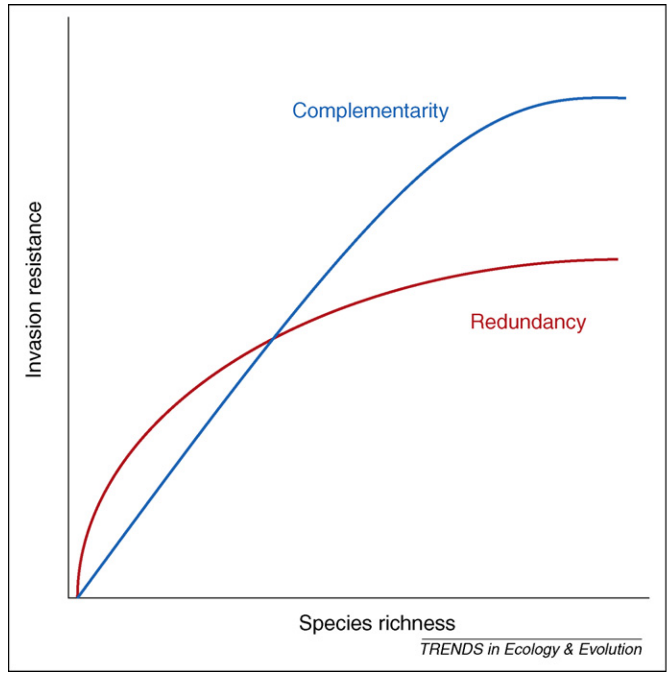

Figure 1. Functional redundancy and complementarity can influence invasion resistance in different ways. Increasing functional diversity (complementarity) can increase invasion resistance by reducing vacant niches available to new invaders. However, increasing the relative abundance of a few key functional types (redundancy) ensures that some level of invasion resistance will be met if species are eliminated from the system. Increasing functional redundancy, as opposed to functional diversity, could lead to higher resistance at low species richness if the invader is of the same functional type.

Functional diversity and community invasibility

Whereas native communities that are functionally similar to invasive species might be more resistant to invasion through direct competition for resources (limiting similarity), native communities might be vulnerable to invasion if their traits are not well dispersed over available niche space and resources are available for new species to establish. Thus, functionally diverse native communities might be less susceptible to invasion because there are few vacant niches. Trait space analyses can reveal vacant niches that could be filled by new invaders, if they can overcome ecological filters [65] (Box 2). In communities strongly structured by resource complementarity among species or by stochastic climatic or disturbance conditions, functional diversity might limit invasion by many different functional groups [66,67] (Figure 1). In addition, functional redundancy is thought to increase the reliability or stability of a system [7,68,69], which is a desirable objective of ecological restoration. Because species within functional groups can show unique responses to environmental factors and biotic interactions [68], redundancy ensures that at least some members of a functional group will survive severe climatic and disturbance events. Thus, where one or a few invaders (e.g. invasive grasses) threaten restoration success, increasing the relative abundance of a few relevant functional groups might be the optimal strategy.

Several studies have examined the relationship between species diversity and community invasibility and found that results are largely scale dependent. At the landscape scale, invasive and native species diversity

Box 4. Future research directions

Although a trait-based community assembly framework shows great promise for structuring native plant communities in restoration efforts, some outstanding questions remain. These issues present opportunities for fruitful collaborations among restoration practitioners, plant ecologists and community ecologists.

Trait plasticity

Restoration projects that involve multiple changes in resource availability, disturbance or stress might elucidate our understanding of trait plasticity in complex, multivariate environments. Plant fitness will be affected by different traits in different environments. For example, in water-limited habitats, leaf-level water-use efficiency had a greater influence on plant fitness in the annual species *Polygonum persicaria*, whereas in moist environments, root biomass allocation was more closely linked to fitness [86]. Restoration practitioners and ecologists can contribute to our understanding of trait plasticity by assessing the variation in trait values within species across sites differing in microclimate and diversity.

Species interactions

Restoration planning must consider traits of other species present at various stages of restoration. Whereas studies of community assembly largely focus on direct, negative species interactions associated with competition [12], direct and indirect positive interactions among members of different functional groups could be equally important in structuring communities but have received less attention [66,87–89]. By applying an integrative community framework, restoration projects can contribute to our understanding of the relative importance of the processes that influence the potential for success of a species in a given community, including competition, facilitation and recruitment limitation. One way to address this would be to design restoration projects that simultaneously alter multiple filters (e.g. dispersal, competition, soil fertility) and assess the role of each filter (and interactions among filters) on the performance of native and invasive species.

Long-term community dynamics

Many restoration projects suffer from an acute lack of postproject monitoring, which makes it difficult to assess the effectiveness of various restoration protocols. Collaborative examinations of how the application of each of the three theories proposed here (limiting similarity, ecological filter manipulation and functional diversity) improves actual restoration outcomes will benefit both ecologists and restoration practitioners. Ecologists can take advantage of restoration projects to design and implement controls, treatments and long-term data collection/monitoring to follow community succession and temporal dynamics. Follow-up in the form of ecological data collection also provides monitoring of project outcomes for the benefit of practitioners.

are positively correlated [70–72]. This is because plant diversity is controlled more strongly by soil fertility, disturbance intensity and seed density than by competition at these large scales. By contrast, at the local scale, susceptibility to invasion can decrease with increasing species diversity [44,72,73] as a result of competitive exclusion or by increasing the likelihood of including strong competitors or biotic controls of the invaders [66,67,74]. The opposite pattern, a positive relationship between invasibility and diversity, can occur if facilitation (e.g. nitrogen fixers) or disturbance strongly influences species diversity at these local scales [48,71,75,76]. Despite these emerging patterns, a recent analysis of the diversity–invasibility literature suggests no general relationship between species diversity and community invasibility at either landscape or local scales [11]. For the purposes of restoration, this finding suggests that the specific functional composition of the native community (e.g. resource-use traits, phenology, flammability) is likely to be more important than community diversity (e.g. species richness).

Conclusions

The increasing need to reassemble communities through ecological restoration provides an opportunity to apply a community assembly framework to help restored communities resist invasion by exotic species. As many restoration efforts are stymied by invasive species, the trait-based framework that we advance here will have wide-reaching implications for restoration success. Large-scale restoration projects are needed to test this conceptual framework. Specifically, projects that select native communities based on trait similarity to existing and potential invaders or that alter ecological filters based on differences in key traits among natives and invasives will be most useful in testing this framework. These projects will also contribute to fundamental, unresolved issues in the fields of plant and community ecology (Box 4). As highlighted in this review, exploring assembly processes in the context of ecological restoration efforts can increase our understanding of the relative importance of recruitment limitation, facilitation, competition and environmental factors in community assembly.

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