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Biodiversity in changing environments: An external-driver internal-topology framework to guide intervention

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Abstract

Accompanying the climate crisis is the more enigmatic biodiversity crisis. Rapid reorganization of biodiversity due to global environmental change has defied prediction and tested the basic tenets of conservation and restoration. Conceptual and practical innovation is needed to support decision making in the face of these unprecedented shifts. Critical questions include: How can we generalize biodiversity change at the community level? When are systems able to reorganize and maintain integrity, and when does abiotic change result in collapse or restructuring? How does this understanding provide a template to guide when and how to intervene in conservation and restoration? To this end, we frame changes in community organization as the modulation of external abiotic drivers on the internal topology of species interactions, using plant–plant interactions in terrestrial communities as a starting point. We then explore how this framing can help translate available data on species abundance and trait distributions to corresponding decisions in management. Given the expectation that community response and reorganization are highly

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complex, the external-driver internal-topology (EDIT) framework offers a way to capture general patterns of biodiversity that can help guide resilience and adaptation in changing environments.

KEYWORDS
coexistence, conservation, environmental climate change, functional traits, networks, plant community, restoration, species interactions, temporal dynamics, time series

PHOTO 1. Katharine N. Suding, recipient of the 2018 Robert H. MacArthur Award.

INTRODUCTION

Accelerating global change, including both directional changes (e.g., warming) and increased variation or extremes (e.g., droughts and deluges), is receiving well-justified attention from scientists and policy makers (Collins et al., 2014; Field et al., 2014). Although great effort is focused on managing the climate crisis (Steffen et al., 2018), we face a biodiversity crisis that is equally profound (Díaz et al., 2019). Biodiversity is declining faster today than it has at any previous point in human history (Ceballos et al., 2020), with current extinction rates far outpacing speciation (De Vos et al., 2015). By 2050, climate-induced habitat alteration is predicted to result in the extinction of a third of the species on this planet (Roman-Palacios & Wiens, 2020). Despite strong evidence of nature's benefits to people (Pecl et al., 2017) and a deep moral imperative (Callicott, 2013), we have not made comparable progress advancing models of biodiversity change, particularly at scales relevant for local management action (Díaz et al., 2019).

Against the backdrop of globally elevated extinction rates (Ceballos et al., 2020; Pecl et al., 2017), local biodiversity change (within a terrestrial nature reserve or marine protected area, for instance, where we expect most species to have the potential to interact with one another) is often idiosyncratic: Some areas are losing species, other areas are gaining species, and still others are surprisingly resilient (Chase et al., 2019; McGill et al., 2015; Srivastava et al., 2021). One of the few generalities is species turnover and shifts in abundance (Blowes et al., 2019; Dornelas et al., 2014; Vellend et al., 2017), reorganizing communities through time.

The multitude of ways ecological communities reorganize exposes the limits of our ability to predict biodiversity response and plan interventions to guide that change (Hobbs et al., 2017; Lynch et al., 2021; Srivastava et al., 2021). Species turnover within protected area boundaries defies the strong spatial roots of conservation (Nicholson et al., 2021), traditionally well versed in maintaining diversity within a defined place (Bergstrom et al., 2021; Pimm et al., 2018). Further, community reorganization in response to environments with no prior analog defies the temporal roots of ecological restoration, built on foundational concepts of recovery, succession, and assembly back to a prior state (Palmer et al., 2014; Suding, 2011). As suitable habitats shift, baselines change, and reference states blur, we need information to guide decisions about possible interventions and thier effect on trajectories of community reorganization (Hobbs et al., 2011; Prober et al., 2019; Shackelford et al., 2022; Suding et al., 2015).

Generalizing local biodiversity response to global environmental change is an incredible challenge, yet it can be informed by several rich bodies of work. First, understanding relationships between the environment and species composition, both temporally and spatially, has been a theme in ecology since its inception (e.g., Clements, 1916; Gleason, 1926). A second body of work, often intersecting with the first, has considered how species interactions structure communities and maintain diversity (Leibold, 1995; MacArthur & Levins, 1967; Tilman, 1994). Functional traits have emerged as a complementary third approach to better understand the mechanisms by which species respond to the environment and each other (Adler et al., 2012; HilleRisLambers et al., 2012; Usinowicz & Levine, 2018). A key challenge is to account for both the direct effects of the environment and the indirect effects of the environment moderated by interactions among species (Gilman et al., 2010; Suding et al., 2008; Tylianakis et al., 2008; Tylianakis & Morris, 2017).

Research across all three bodies of work supports the expectation that global environmental change will almost invariably drive changes in the organization of biodiversity within a community, including the number (through gains and loss) of species, their identity (through compositional turnover), and their abundances (becoming more abundant or rare), as well as how species interact together (who is interacting with whom, type of interactions, per-capita interaction strengths). This expectation shifts the key question in biodiversity change from *whether* a community will reorganize to *how* that reorganization will play out through time (Avolio et al., 2020; Langley et al., 2018). Simple biodiversity metrics (e.g., richness) often provide little insight into the important shifts that emerge (Godsoe et al., 2023), as reorganization has many flavors: It can be compositional turnover and reshuffling of species abundances that adaptively track global change or it can be wholesale transformations with cascading species loss (Hillebrand et al., 2018). Intervention to redirect this reorganization, when it is desired, needs to target these different pathways.

Here we develop a generalizable, four-step framework that captures community reorganization in a way that supports the management of local-scale biodiversity dynamics. First, we propose two primary axes influencing biodiversity response—external drivers and internal topologies (the structure of species interaction networks)—and suggest a systematic way to generalize this variation. We then identify research approaches (e.g., data collection and analyses) that can build an understanding of community reorganization across these axes to support strategic management interventions. Third, we illustrate this approach in different ecosystems that vary in their external drivers and their internal topologies. Lastly, we provide a pathway for application to management, emphasizing the ties between different elements in the framework and interventions. We end with some key uncertainties and paths forward from here. In this initial conceptualization, we focus on interactions within a single trophic level (e.g., plants interacting with plants) and define a community according to this within-guild framing. It will critical to expand this initial framing to other taxa (e.g., beyond plants) and other interactions (e.g., food web, plant–pollinator). We also acknowledge the many advances at eco-evolutionary and ecosystem interfaces, as well as at regional scales related to species movements and range shifts, that are very applicable but beyond the scope of this paper.

A TEMPLATE FOR LOCAL BIODIVERSITY CHANGE

While we have made great progress in understanding patterns of local biodiversity change (e.g., McGill et al., 2015), the lack of a general template to understand how environmental change is reorganizing a community can lead protected-area managers to make decisions more focused on avoiding any further reorganization than on guiding a system toward a particular trajectory (Cook et al., 2013; Yates et al., 2018). Our experience suggests that key to identify important mechanisms is to consider how external drivers modulate internal topologies—which we call the external-driver, internal-topology (EDIT) framework.

The EDIT framework is aimed at contextualizing shifts in biodiversity as a community reorganizes in response to global environmental change (Figure 1). First, communities often exhibit distinct responses to different external drivers (e.g., higher temperature vs. variation in rainfall) because the abiotic conditions created by the drivers lead to specific functional responses (Avolio et al., 2021). While these external drivers are typically "slow variables" that change independently of internal dynamics (Scheffer, 2009), they modulate community organization via the internal network structure of interacting organisms, which we call topologies (after Kéfi, 2020; Petchey et al., 2009, among many others). We draw from network ecology here, noting that most usage of topologies has been largely in consumptive (food web) or nontrophic multilayer (plant–pollinator) networks focused on who interacts with whom; we widen this usage with consideration of the direction and strength of interactions important in competitive networks (e.g., Soliveres et al., 2015). As topologies are repeatable nonrandom configurations of structure, they provide generalization of the interactions that characterize a particular community and how external drivers may shift that structure (Cadotte et al., 2013; Lasky et al., 2014; Letten et al., 2017; Pascual & Dunne, 2006).

The EDIT framework borrows concepts from complexity science (e.g., Meadows, 2008) and stands on the shoulders of ecological giants: Lindeman (1942) used a similar representation for ecosystem trophic dynamics (also Sterner, 2012), Paine (1966) in food webs, and MacArthur (1972) and May (1974) in their theoretical constructs. A defining characteristic of the EDIT framework is that it aims to support local managers who are navigating the

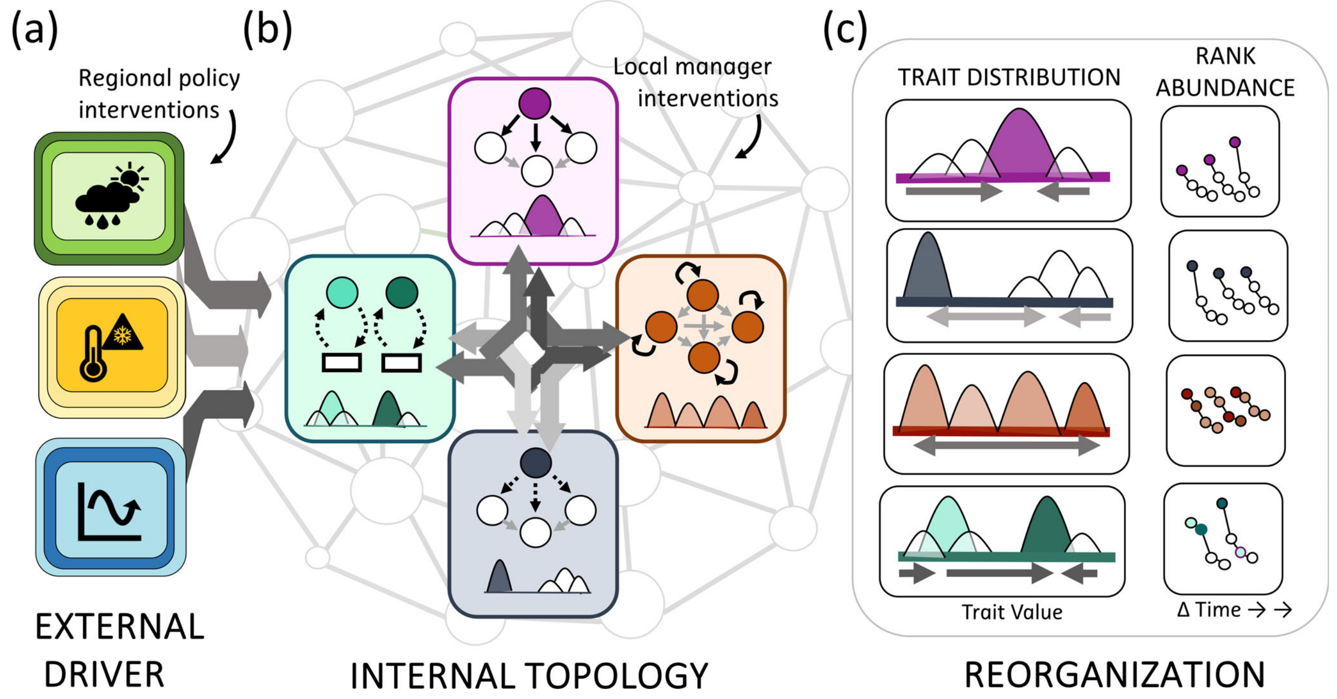

FIGURE 1 Framing local biodiversity response to global environmental change by (a) types of external drivers (top to bottom: resource, green icon; stress, yellow; variability, blue) and (b) internal species interaction topologies (clockwise: dominance, purple; negative frequency, brown; facilitative, gray; positive feedback, teal) allows for (c) a general set of predictions of community reorganization (left to right: trait distributions, species rank abundance curves through time). It distinguishes the type of interventions commonly made at the local level (b) from those at the regional policy level (a). Internal topologies are depicted with key species groups (circles) linked by important interactions (dark solid arrows indicate negative, dotted arrows indicate positive, and looped arrows indicate intraspecific interactions). Patterns of trait distributions (with the amplitude of the curve indicating the abundance of species and the mean and variability of trait values along the *x*-axis) can be diagnostic of particular topologies (in b). Community reorganization (c) can involve changes in the number (through gains and loss) of species, their identity (through compositional turnover), and their abundances (becoming more abundant or rare); here we show how trait distributions and rank abundance curves (abundance of species ranked by abundance, with curves at different time steps) may change over time with particular drivers: see Tables 1 and 2 for specific expectations.

complexity of the biodiversity and global change crises by creating a generalizable template that can apply to a diversity of ecosystems. By using accessible data sources—from long-term patterns of abundance in monitoring, to results of experimental manipulations and management trials, to functional trait characterizations of species composition—multiple forms of inference can capture community reorganization (Adler et al., 2013; Case & Bender 1981; Funk et al., 2017; Ives et al., 2003; Suding et al., 2008; Wootton, 1993). Here, we highlight three types of external drivers and four internal network structures that we expect to be common in terrestrial plant communities (Figure 1).

External drivers

Climate change and associated changes in atmospheric deposition and disturbance regimes impact ecosystems by shifting both mean conditions and environmental variability (Dickinson et al., 2014; Smith et al., 2009). Although a large body of work emphasizes the importance of external drivers on community dynamics, it is often difficult to link local-scale climate factors with the reorganization of a community over time (Antao et al., 2020; Vellend et al., 2017). These difficulties often stem from climate variables affecting species through a variety of pathways and environmental drivers varying in importance across systems (Avolio et al., 2020; Felton et al., 2021; Harrison, 2020). One way to generalize across external drivers is to frame them in the context of major controls on species fitness (selection after Vellend [2017]): (1) those that shift the availability of limiting resources, (2) those that increase stress via changes in nonresources, and (3) those that increase the variability in resource availability or stress conditions (Figure 1a, Table 1a). In what follows, we briefly discuss expectations for the direct effects of external drivers for each of these three types of drivers (we consider indirect effects through

TABLE 1 Framing community reorganization to global environmental change by external drivers (a) and internal network topology (b), with predictions of demographic response, functional trait response, and possible local management interventions.

Type	Demographic response[a]	Functional response	Local management interventions[b]	
			To direct	To resist
(a) External drivers				
Resource	Increase population growth (assuming resource is limiting)	Benefit resource acquisitive species, disadvantage resource conservative species	Add resources (e.g., fertilize)	Decrease available resources via biomass-removing disturbances (grazing, fire) or microbial immobilization (via C additions for N)
Abiotic stress	Decrease population growth	Benefit stress-tolerant/avoidant species	Restrict nonresource amelioration (e.g., temperature management, shading) that would alleviate stress	Prioritize enhancement of foundation/nurse species or physical structures (e.g., zeedyk structures), alleviate stressors
Environmental variability	Decrease population growth	Benefit species with bet-hedging and/or plastic traits	Limit regulation of environmental fluctuations (e.g., flow regimes) or resource inputs (e.g., irrigation)	Develop adaptive management plans to reduce exacerbating factors in times of extremes (e.g., adjusting grazing pressure)
(b) Internal network topology				
Dominance	Skew of per-capita interaction strengths, with a few strong negative interactions, deterministic hierarchy, or higher-order interactions	Increase representation of high resource optimal traits; decrease or loss of species with traits far from resource acquisitive optimum	Act to increase fitness of dominant plant through interventions that target other species	Introduce selective disturbance agents that target dominant species and/or desirable species with high niche overlap and trait optima with dominant
Facilitative	Skew of per-capita interaction strengths, with a few species (nurse plants) exerting strong positive effects on beneficiary species	Increase representation of traits that benefit from nurse facilitation (less stress tolerant); nurse plant traits include abiotic tolerance, aboveground stature, and traits that affect abiotic or biogeochemical conditions	Promote nurse plant recruitment and persistence up to moderate densities, introduce desirable species that could otherwise not persist without nurse plant	Remove nurse plants
Negative frequency	Self-limiting negative frequency dependence (advantage when rare); strong negative conspecific interaction strengths	Broaden trait representation related to niche partitioning; loss of species with high trait/niche overlap	Remove undesirable species with high niche overlap, introduce species dissimilar to residents with low overlap	Limit abundance fluctuations, homogenize environmental variation and fluctuation
Positive feedback	Self-reinforcing positive frequency dependence, advantage when abundant; priority effects; strong positive conspecific interaction strengths	Trait overdispersion (bimodal distribution) at larger scales due to local priority effects; advantage of traits related to positive cross-trophic feedbacks (plant–soil, plant–pollinator)	Protect areas from biomass-removing disturbance to maintain desirable feedbacks	Reduce biomass and legacy effects alongside new species introduction to shift priority effects

Note: These should be treated as hypotheses, consistent with theory but in need of testing in experimental settings and in practical application. See text for definitions and more explanation for each driver and topology.

[a] For external drivers, expectations of direct effects of increasing intensity (e.g., increased resource availability) with the opposing patterns valid for decreasing levels of external drivers. For topologies, expectations of intensification or shift to topology (e.g., toward increased dominance control).

[b] We describe these in the context of resist–accept–direct (RAD) framework for decision making, after Lynch et al. (2021), where a third option for each is to accept (do nothing).

internal dynamics in the following sections), acknowledging the large amount of prior work on these core ecological concepts, the sometimes fuzzy expectations related to the separation of direct and indirect effects, and the many potential avenues of expansion.

Resource availability

Many aspects of environmental change can be viewed as changes in resource availability (green icon in Figure 1a): Notable for terrestrial plants are rainfall in water-limited, atmospheric nitrogen (N) deposition in N-limited and eutrophication in phosphorus-limited systems. Resource limitation is classically defined by a change in a resource that leads to an increase in production. Changes in multiple resources can also occur simultaneously, thereby colimiting plant production (Bloom et al., 1985; Farrior et al., 2013; Seastedt & Knapp, 1993). When solely considering the direct effects of external drivers, an increase in the availability of limiting resources should increase population growth rates and abundances of all species, albeit to different extents (e.g., Dıaz et al., 2003; Ives & Cardinale, 2004). Plants with traits related to rapid resource consumption and growth, described as a resource acquisitive syndrome, are thought to benefit most from the direct effects of increased resource availability, whereas a resource conservative syndrome of traits is thought to characterize plants able to persist as resource availability declines (Goldberg, 1990; Tilman, 1982).

Abiotic stress

Environmental change can increase plant stress through physiological pathways that are not driven by depletable resources (e.g., yellow icon in Figure 1a). One clear way to define plant stress was made by Grime (1979), who argued that stress limits the ability of plants to convert energy into biomass. For instance, low or high temperature, anoxic conditions, high salinity, heavy metals, and ultraviolet light have often been considered abiotic stressors for plants (Chapin et al., 1993). As opposed to increased population growth rates in response to increased resources, stress is expected to directly decrease population growth rates. Species will be less impacted by stress if they can tolerate (e.g., via resource conservative traits protecting plants from tissue damage), avoid (e.g., via altered physiology or growth), or escape (e.g., via early or late phenology) increasing levels of stress (Ives & Cardinale, 2004; Wardle & Peltzer, 2003). The distinction between abiotic stress and resource limitation is imperfect: Low water resource conditions (e.g., drought) are also commonly considered a stress that affects photosynthetic capacity, and some stressors (e.g., temperature) can affect resources, such as nitrogen availability, through microbial processes.

Environmental variability

We propose a third type of external driver related to a shift in the historic range of variability experienced by a system (blue icon in Figure 1a; Sala et al., 2015; Vazquez et al., 2017). Extreme events, such as increased rainfall and temperature variability, can affect the proportion and timing of suitable growing conditions for a given species and can cause the community reorganization responses to lag behind the shift in environmental conditions (Lawson et al., 2015). Population growth is often expected to decrease in cases of increased environmental variability (see Drake [2005] and Rudgers et al. [2018] for more detailed treatment). Increased demographic stochasticity can accelerate this decline by elevating the chance a population reaches a low-abundance threshold with high extinction risk (Gravel et al., 2011). Species with bet-hedging and highly plastic traits are thought to better tolerate increased variability, depending on whether variability is predictable or stochastic, often at the cost of lowered arithmetic mean fitness (Botero et al., 2015; Simons, 2011).

Summary

Parsing the complexity of external forcing associated with global change into three types of external drivers is a clear simplification. Yet, this generalization facilitates the connection of emerging climate exposure and sensitivity studies (e.g., Dickinson et al., 2014) to decades of theory and knowledge development around core concepts of resource availability, abiotic stress, and increased temporal variability (Flores-Moreno et al., 2019; Gravel et al., 2011; Hart & Marshall, 2013). This lens enables broad inference into the type of species (and their traits) that are likely to respond directly to a given type of external driver.

Internal network topologies

Species interactions are dynamic, varying across species, space, and time via the structure of interactions that compose an ecological network (Figure 1b; Gilman et al., 2010; Losapio et al., 2019; Pellissier et al., 2018; Tylianakis & Morris, 2017; Zoller et al., 2023). Networks can be represented with nodes as species (or other component groupings based on, e.g., traits or abundance) connected by links that represent interactions (and the strength of these interactions) between nodes. Networks assemble in nonrandom sets of topologies, possibly resulting from selection against unstable configurations or emerging from properties of interacting species (Kéfi et al., 2015; May, 1974; Paine, 1980). A network topology can provide insight into important pathways that characterize community reorganization, for instance, whether a given structure is maintained or when a shift occurs to a contrasting network structure (Pascual & Dunne, 2006; Ponisio et al., 2019).

The translation of complex internal dynamics to network topologies enables the identification of structures that inform common mechanisms of (and management solutions for) community reorganization (Bascompte, 2010; Bhatia et al., 2023; Cenci et al., 2018; Delmas et al., 2019; Dormann et al., 2017). Here we develop a set of topologies that describe interaction structures common in terrestrial plant communities that also translate to theories of species' interactions, for example, differences in average fitness and frequency dependence after Chesson (2000), Grainger, Letten, et al. (2019a), Letten et al. (2017), and many others. We propose four general types of network topologies: dominance control, facilitative control, negative frequency control, and positive feedback control (Figure 1b, Table 1b).

Dominance control

A competitive hierarchy orders species by their ability to obtain limiting resources and, in doing so, negatively affect the fitness of other species (Figure 1b: purple symbol; Matias et al., 2018; Wainwright et al., 2019). Optimal traits related to competitive ability confer high relative fitness (Hardin, 1960) and increased dominance in competitive hierarchies (Figure 1c; Kraft et al., 2015; Perez-Ramos et al., 2019). Species with suboptimal traits are more likely to be excluded. This type of topology often has a skewed distribution of interaction strengths, with a few abundant species having strong competitive effects, in terms of per-capita interaction strengths, total interaction strengths (abundance × pre-capita interaction strengths), or often (we suspect) both. Interactions among other species are weak and potentially intransitive without a consistent ordering (Paine, 1992; Preston et al., 2019). Dominance could also arise through higher-order interactions such as negative interactions between less abundant species that benefit a third species. We call this network topology dominance control (Table 1b, purple icon in Figure 1b).

Facilitative control

Positive interactions have been increasingly recognized as critical components in interaction network structure (Bruno et al., 2003; Bulleri et al., 2016). Nurse plants are often considered foundation species that enable the persistence of other species through mechanisms such as soil moisture retention, soil nutrient modification, abiotic stress amelioration, seed trapping, pollinator visitation, and herbivore protection (Brooker et al., 2008; Filazzola & Lortie, 2014; Gomez-Aparicio, 2009). These positive interactions can expand species niches through increasing average fitness. Like dominance control, the direct effects of external drivers are often assumed to lead to nurse plant abundance, while the interactions with the nurse plant determine persistence of the other species (Brigham & Suding, 2023). Traits that allow for the persistence of nurse plants are expected to differ from the traits that allow for the persistence of the beneficiary species, resulting in high trait dispersion and clustering (Schob et al., 2012). This type of topology also should have a skewed distribution of interaction strengths, with a set of species (e.g., nurse plants) positively affecting the growth rate of beneficiary species. Interactions among beneficiaries may often be weaker and more negative. We call this topology facilitative control (Table 1b; gray icon in Figure 1b).

Negative frequency control

Self-limitation or negative frequency dependence occurs when differences in species resource use cause intraspecific interactions to be more intense than interspecific interactions. As a result, when any one species increases in abundance, it interacts more with conspecifics, and its per-capita growth rate slows (Figure 1b: brown symbol; Dostal et al., 2018; Grainger, Levine, & Gilbert, 2019b; Hallett et al., 2018). When interactions are largely structured by negative frequency dependence, species have high growth rates when rare and slowed population growth when abundant, fostering the persistence of multiple species (stabilizing mechanism after Chesson, 2000). Networks structured by negative frequency control are thought to have high functional diversity and low niche overlap (Figure 1b; HilleRisLambers et al., 2012; Kraft et al., 2015). As similar negative frequency dependence can occur due to interactions with other trophic positions as well, such as through the role of host-specific enemies (Bever, 1994; Johnson et al., 2017). Networks with this structure have strong negative conspecific associations, with weaker interactions across heterospecific associations (and possibly more intransitivity; Yang & Hui, 2020). We term this type of topology negative frequency control (Table 1b, Figure 1b in brown).

Positive feedback control

Positive frequency dependence occurs when a species has an advantage as it becomes more abundant. Mechanisms include self-reinforcing effects on soil communities, resource cycling, or trophic interactions (Figure 1b, teal symbol; Suding & Hobbs, 2009). Positive feedbacks can accelerate compositional change and cause community divergence into alternative states (Bachelot et al., 2020; Chung et al., 2019; Larios et al., 2017). With positive feedback control, species arriving first have an establishment advantage (priority effect) and the ability to modify environments (Figure 1b: teal symbol; white boxes) in a way that favors their continued performance over others (Song et al., 2020; Yelenik & D'Antonio, 2013). Subsequent community divergence results in patchiness and overdispersed bimodal distributions of traits at larger scales (Figure 1c bottom row, arrows pointing toward divergent trait optima; Fukami et al., 2005). Networks with this structure have positive effects among conspecifics, particularly for species exhibiting self-reinforcing effects. Weaker interactions are expected to occur among heterospecifics, with potentially diverging positive or negative effects from the modifying species. We call this topology positive feedback control (Table 1b, teal icon in Figure 1b).

Summary

The influence of internal dynamics is widely viewed as a key reason for the difficulty in predicting local diversity change (Chen et al., 2019; McGill et al., 2015). The four types of interaction topologies detailed above—dominance, facilitation, negative frequency, and positive feedback—are common expectations for contrasting structures that can enable generalization of internal dynamics. These four topologies also array along gradients related to niche and fitness differences (similar to Spaak et al., 2021), with dominance to facilitation along a fitness axis (where traits affect per-capita growth rate regardless of species frequency) and positive to negative frequency control along a niche axis (where frequency and the similarity of traits relative to others affect per-capita growth). Networks with a weak or random structure of interactions that do not fit in these bins could be considered either additional topologies (e.g., neutrality or strong abiotic control) or transient states due to slow dynamics or disequilibrial lags (CaraDonna et al., 2021; Williams et al., 2021). More work on the assembly and disassembly of topologies will better illuminate these dynamics over time (Bascompte & Stouffer, 2009).

External drivers modulating internal topologies (EDIT)

While network structure has often been treated as a static system characteristic, accumulating evidence indicates that external drivers can indeed change the structure of species interactions (Table 2; Poisot et al., 2015; Valiente-Banuet et al., 2015). For instance, a community that is resilient to changes in external drivers might often persist in its current topology following disturbance, with moderate changes in interaction strength among species. In contrast, when external drivers shift the community into a different topology (e.g., from negative frequency to dominance control), it may often lead to community transformations with more abrupt shifts in composition, richness, and the distribution of functional traits (e.g., Cenci et al., 2018; Landi et al., 2018).

Expectations for terrestrial plant communities suggest common pathways by which external drivers can mediate internal dynamics to shift topologies (Table 2, Figure 1b internal arrows). Increasing resource availability (e.g., nitrogen deposition) is expected to directly benefit species that rapidly acquire resources and grow fast and shift topologies toward dominance control (Matias et al., 2018; Olsen et al., 2016; Wainwright et al., 2019). Increasing stress is predicted to harm tolerant species the least and shift topologies toward facilitative control (i.e., the stress gradient hypothesis; le Roux & McGeoch, 2010; Maestre et al., 2009). Increasing environmental variation can directly benefit bet hedging and plastic species, while shifting topologies toward negative frequency control with increased importance of niche differences (Adler & Drake, 2008; de Mazancourt et al., 2013); it may also shift organization from dominance to facilitative control during stressful times such as droughts (Ploughe et al., 2018). Positive feedback topologies are often expected at intermediate resource or stress conditions and then lead to threshold behavior as resource availability or stress conditions intensify (Dudney et al., 2018; Larios et al., 2017).

Summary

External drivers are expected to moderate internal dynamics, potentially shifting one topology toward another (gray arrows in Figure 1b). We expect that shifts in topology might often constitute more substantial community reorganization and indicate a loss of resilience. We note here that these more substantial shifts could align with conservation or restoration goals or they might be considered catastrophic collapses. Approaches

TABLE 2 External drivers modulate internal dynamics in several ways depending on potential for external drivers to shift internal network topologies.

		Local management to either direct or resist shift[a]	
Modulation	**Indicators of shift**	**To direct shift**	**To resist shift**
Resource driver shifts other topologies to dominance control	Enhanced resources foster dominance and increased niche overlap; trait overdispersion shifts to trait under dispersion centered at trait optima	Selective disturbance or removal targeting resource acquisitive species, in combination with resource reduction measures, or the addition of fluctuating environmental conditions (e.g., through varied disturbances)	Ensure representation of species with trait optima (resource acquisitive), aid resource retention; consider opportunities to diversify along other axes (e.g., phenological, bet hedging)
Stress driver shifts other topologies to facilitative control	Persistence of species in proximity of nurse plants, divergence of functional diversity into nurse and beneficiary clusters	Plant nurse plants at intermediate densities	Remove nurse plants and augment/add species that can persist without need for positive interactions
Variability driver shifts other topologies to negative frequency control	Fluctuating conditions diversifies niche space, fostering negative frequency dependence and reducing niche overlap while increasing functional dissimilarity	Establish diverse communities with low niche overlap, initially monitor and aid persistence of dissimilar and rare species in their "bad" times (e.g., by restoring storage mechanisms [seed or bud banks])	Maintain desired trait optimum (e.g., resource acquisitive and productive species) by selecting or supporting species that also exhibit high trait adaptability (e.g., high plasticity); reduce variability through resource additions in "bad" times (fertilizer, irrigation)
Stress and resource drivers shift positive feedback control to other topologies	Both increased abiotic stress and increased resource availability reduce priority effects and increase trait determinism; positive feedback control operates in intermediate stress/resource conditions	Target species for removal that have strong positive feedbacks, address legacy effects in soils or trophic communities to disrupt feedbacks, aid in vegetation shift consistent with resource or stress driver	Avoid patch-removing disturbances that reset priority effects

Note: Here we list several expectations of how particular external drivers may shift topologies. A shift may or may not be desirable, depending on management goals. Communities can also reorganize (e.g., in composition or abundance rankings) and maintain a particular topology.

[a] We describe directing and resisting these shifts following resist–accept–direct (RAD) framework for decision making (Lynch et al., 2021), where a third option for each is to accept the shift.

to infer network structure through species associations or functional trait proxies, which we detail in the next section, could help identify decision-making points.

APPROACHES TO INFER DRIVERS AND TOPOLOGIES

One value of a general heuristic framework is that it can be used with differing levels of knowledge and information, allowing multiple types of users and application in diverse systems. Research approaches vary in generality and certainty, allowing flexibility in how the framework can be applied. We detail three main ways of collecting and applying data in this framework to understand community reorganization over time and point to efficacious management interventions.

Experimental manipulations of external drivers and internal interactions

Understanding internal interaction structure in communities has long relied on experimental approaches, such as pairwise comparisons or species removals (Allesina & Tang, 2012; Grilli et al., 2017; Levine et al., 2017). While these approaches may be infeasible in conservation or restoration settings, they provide precise, causal estimates of species interactions. For instance, pairwise interaction trials (without varying the frequency of one species relative to another, e.g., 0:1, 1:1, 1:0) are used to estimate per-capita competitive hierarchies and facilitative effects. Varying the frequency of pairwise species interactions (e.g., 1:9, 5:5, 9:1) allows for direct tests of some types of structure (negative frequency control, positive feedback control). "Invasion when rare" is a complementary approach often used to identify frequency dependence (e.g., when an individual performs better when invading communities/patches dominated by conspecifics rather than heterospecifics, or vice versa).

Each of these approaches can be extended to address how external drivers modulate internal topologies. We have used "invasion when rare" approaches, for instance, to determine feedbacks and alternative states in California grasslands along a gradient of nitrogen availability (Larios et al., 2017) and density/frequency gradients combined with rainfall manipulations to determine mechanisms of coexistence on California rangelands (Hallett et al., 2019). While these approaches are time-intensive and often allow for only a subset of species and environmental conditions to be considered, they are a direct way to estimate the structure of interaction networks and how external drivers can change that structure to lead to biodiversity change (Maynard et al., 2020; Perez-Ramos et al., 2019; Wainwright et al., 2019).

Inference with long-term observational data

Various approaches to inferring drivers and internal topologies from observational multispecies data sets exist, including population demographic (Farrer et al., 2014; Tredennick et al., 2017), multivariate autoregressive (Ives et al., 2003; Hampton et al., 2013), S-map (Sugihara et al., 2012), multivariate joint species distribution (Ovaskainen et al., 2017), and other related models (Clark et al., 2020; Weiss-Lehman et al., 2022). While the specifics of these methods vary, they share the general approach of partitioning the spatiotemporal variation in community data sets to components that relate to the effects of environmental characteristics, species interactions, and random processes. They approximate species interactions as pairwise associations within a sampling unit (e.g., a negative per-capita association would be indicated if one species increased while another one decreased, after variation due to environmental effects was taken into account). These pairwise associations can be compiled into a matrix describing the associations of each species with every other, with the diagonal indicating intraspecific effects. Topologies can be broadly inferred from these matrices; for instance, self-limitation would be indicated by strong negative strengths in diagonal elements, and skewed distributions would be indicated by a few strong and many weak associations across the matrix. Comparisons at different points in time and across space (e.g., reference and managed sites) allow inference of community dynamics and management effects.

There are many reasons why correlative studies describing drivers and interactions from observational data should be interpreted cautiously, including the underlying challenge that correlations can fail to capture causal drivers and will miss higher-order interactions (Blanchet et al., 2020; Godwin et al., 2020). While there are constraints in interpretation, these rapidly developing methods allow a bridge between theory and a common type of data set within the management community: repeated monitoring of local community composition. We have used observational data, combined with demographic modeling approaches, to infer the mechanism of frequency control in serpentine grasslands, for instance (Hallett et al., 2019), and a hybrid approach where we manipulated external drivers experimentally and inferred internal interactions with hierarchical modeling in alpine habitats (Collins et al., 2022). We provide more details of these examples in the following section.

Inference with functional traits

Functional trait frameworks are a burgeoning research area in ecology, and there is potential to expand their use as a diagnostic of the type of external driver and topology associations with reorganization dynamics (Cadotte et al., 2013; Dwyer & Laughlin, 2017; Zirbel & Brudvig, 2020). Monitoring shifts in functional traits at the community level (e.g., community-weighted means) can help identify the influence of key external drivers (e.g., increasing representation of stress tolerant or resource acquisitive traits might point to the predominance of a stress or resource driver, respectively). Comparing changes in functional trait distributions can help identify internal topologies (e.g., converging to a trait optimum would be consistent with dominance control, while the increasing breadth of trait values would suggest negative frequency control; Figure 1c) (de Bello et al., 2021; Flores-Moreno et al., 2019; Guimaraes, 2020).

Utilizing functional trait information, while promising, also warrants careful consideration. One important and challenging step is to identify traits with measurable fitness consequences related to external drivers and internal topologies in a system (Larson et al., 2015; Laughlin & Laughlin, 2013). While there has been a lot of work exploring traits related to resource availability as an external driver, traits related to abiotic stress (e.g., tolerance and avoidance traits) and environmental variability (e.g., plasticity bet-hedging traits) have been less studied. In addition, traits at the seed and seedling stage rather than adult life history may be especially relevant in response to variability and stress drivers (Larson et al., 2023). Like traits related to external drivers, the predominance of assessing functional traits consistent with one type of topology may overlook the possibly of other types of internal dynamics. In particular, traits that reveal mechanisms of positive frequency dependence in feedback control or that are associated with positive interactions in facilitative control are understudied. As these gaps are filled, functional trait information offers a strong complementary approach, alongside abundance-based species information, to understanding external drivers and internal topologies contributing to biodiversity change.

Summary

Several methods enable inference of external driver and internal topologies in a community, including experimentation, long-term monitoring data, and statistical modeling, complemented by functional trait information. Inference from these approaches can be bolstered by intuition and place-based experiential knowledge of managers, local stewards, and indigenous peoples. Together, these multiple forms of inference can develop a template for identifying external drivers and internal topologies important to community reorganization as well as point to which types of interventions, if any, may be effective in guiding dynamics along desired trajectories.

APPLYING THE EDIT FRAMEWORK: COMBINING EXTERNAL DRIVERS AND INTERNAL TOPOLOGIES TO UNDERSTAND LOCAL BIODIVERSITY CHANGE

Characterizing how internal topologies mediate responses to external drivers can be done using several approaches; all will allow insight into how a community reorganizes in response to global change. Here, we provide three case studies from our work in different terrestrial plant communities, with different approaches, to demonstrate the value of inferring the external driver and changes in the internal topology of interactions in order to better understand and manage community reorganization under global change.

Dominance control in alpine tundra with increased resources (nitrogen, water) in contrast to increased stress (warming)

Observations at Niwot Ridge (Colorado Rocky Mountains, USA) over the last several decades indicate a substantial warming trend, high interannual variability in precipitation (the majority of which falls as snow), and a history of atmospheric N deposition (Crawford et al., 2020). We assessed how three species groups in moist meadow alpine tundra (the most abundant species, a bunchgrass *Deschampsia caespitosa*; the three next abundant species, subdominants; and the next four most abundant species, moderates) respond to experimental manipulations of warming, nitrogen, and snow over 16 years (Farrer et al., 2015; Collins et al., 2022; Figure 2). We used a dynamic competition model (gjamTime; Clark et al., 2020) to infer the direct effects of environmental drivers and shifts in internal interactions on community organization across these global change scenarios.

Under ambient conditions, the tundra plant community was relatively stable, with little change in abundances over time (Figure 2a). Each group experienced strong intraspecific relative to interspecific competition, consistent with a negative frequency topology under ambient conditions (Figure 2d).

Manipulation of an abiotic external driver (warming) shifted a negative frequency topology in ambient conditions toward a competitive reshuffling and dominance control (Figure 2e). While warming exerted only weak direct effects across all species groups, *Deschampsia* experienced increased competition from other species groups under warmed conditions, driven by negative effects of those species on N. As the magnitude of interspecific competitive effects approached that of intraspecific effects, the reshuffling of the competitive hierarchy resulted in increased abundance of several subdominant forb species (Figure 2b) that are emerging as better competitors for limited N under these warmer conditions.

When warming was accompanied by increased snow and nitrogen, external changes also shifted the negative frequency topology in ambient conditions to dominance control, yet in this case they enhanced the success of the most abundant species, *Deschampia*, and caused declines in the other species groups (Figure 2c). Consistent with its increase over time in this treatment, *Deschampsia* positively responded to the external changes, and specifically to increased N availability. We did not detect any direct environmental effects on the other species groups, suggesting their declines were due to internal dynamics. Competitive effects for these other species groups were primarily driven by increased interspecific competition with each other, while *Deschampsia* experienced a reduction in interspecific competitive effects (Figure 2f). This

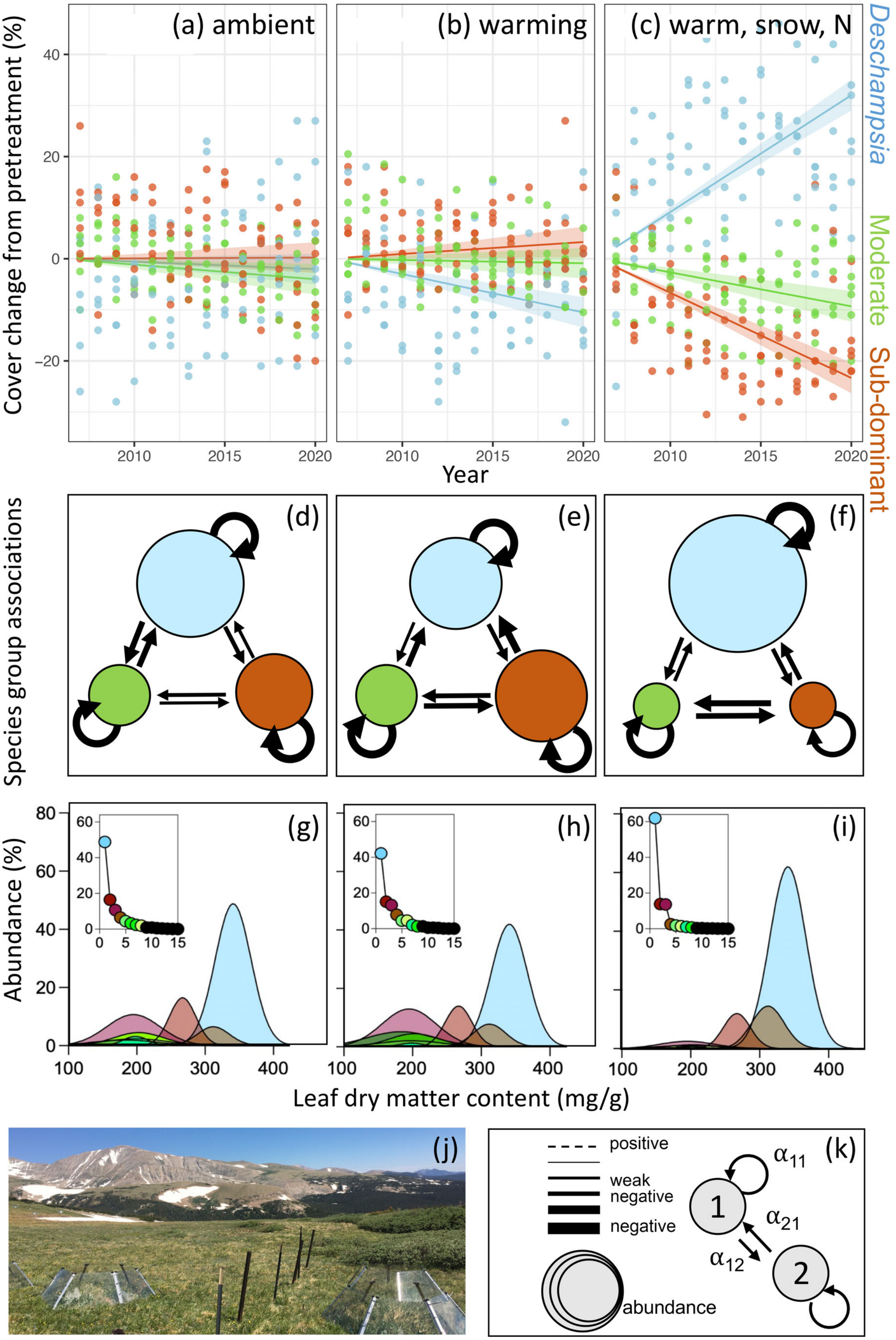

FIGURE 2 Legend on next page.

example also highlights the importance of changes in total interaction strengths (abundance × per-capita effects) that can result from direct positive responses to external drivers such as resource availability.

Viewing how trait distributions shift under these global change scenarios also illuminate the direct effects of external drivers and changes in internal topologies. Under ambient conditions, a wide distribution of functional traits characterizes the moist meadow alpine tundra (Spasojevic et al., 2013; Spasojevic & Suding, 2012), with *Deschampsia* having traits (high leaf dry matter content, tall stature, low specific leaf area [SLA]) characteristic of abundant alpine grasses globally (Figure 2g–i shows the distribution of one trait, leaf dry matter content, as an example). The suite of traits exemplified by *Deschampsia* is thought to lead to high biomass accumulation through lateral spread (Stanisci et al., 2020) and enhanced drought tolerance and freezing resistance (Pescador et al., 2016), particularly when associated with adequate levels of soil N. Warming shifted the trait distribution toward avoidant strategies such as early phenology and lower leaf dry matter content (Figure 2h), supporting the reordering of the competitive hierarchy found by Collins et al. (2022). In contrast, with warming, snow, and N, the trait distribution narrowed toward the trait optima of *Deschampsia*, with reduced abundance of species that have opposing suites of traits, consistent with the intensification of dominance control (Figure 2i).

Negative frequency control in serpentine grassland experiencing climate (rainfall) variability

The serpentine grassland of the Bay Area (CA, USA) supports a diverse set of annual plant species (Hallett et al., 2014; Hobbs et al., 2007) (Figure 3a,b). This system is characterized by highly variable precipitation, which is forecasted to become more variable over time. Hallett et al. (2018), by modeling population dynamics across the six most abundant species, demonstrated that this community was structured by a negative frequency topology. Intraspecific interactions were strong for all species, causing population growth rates to decline as abundance increased. In comparison, interspecific interactions were weaker than intraspecific interactions (Figure 3c,d).

The abiotic driver in this case, temporal variation in rainfall, created favorable and unfavorable conditions for species differently across time. Species with high intrinsic growth rates experienced stronger negative frequency dependence and, consistent with Adler et al. (2012), were less sensitive to the external driver of rainfall variability. This trade-off shifted the network of species interactions in wet and dry years, as some species were more sensitive to rainfall when rare, while others were more sensitive when they were abundant (Figure 3c,d). While species abundances shift with rainfall, functional diversity in such traits as specific leaf area (SLA) were maintained (Fernandez-Going et al., 2012).

Over the last several decades, increased resources through atmospheric N deposition have impacted serpentine grasslands (Eskelinen & Harrison, 2014; Gilbert et al., 2020; Grainger, Levine, & Gilbert, 2019b; Weiss, 1999). As N levels increased later in the time series, an exotic grass, *Bromus hordeaceus*, that was historically moderately abundant and fluctuated with rainfall conditions at low N conditions (Figure 3e,f, orange), was able to increase in abundance in both dry and wet years. Interactions with the historically most abundant species, *Plantago erecta*, indicate strong competitive interactions and a shift toward a dominance control topology

FIGURE 2 Example of dominance control from our work in the alpine tundra. Cover change of the most abundant species (*Deschampsia cespitosa*, in blue), a grouping of the next most abundant three species (sub-dominants, in rust), and the four next abundant species (moderates, in green) over 16 years under (a) ambient conditions, (b) experimental warming (open-top chambers), and (c) warming plus snow (snow fence) and N (addition) conditions. The structure of interactions in ambient conditions (d; see k for legend) suggests dominance control, with asymmetric competitive interactions among the species groups. Warming (a stress driver) shifted the competitive hierarchy to reorder species abundances (e), while the addition of snow and N (resource availability) intensified dominance (f). Panel (k) explains legend for (d–f), where line width indicates strength of associations and circle size indicates relative abundance of each species group (ranging 5%–75% cover). Abundance of each of 15 species as a function of one functional trait, leaf dry matter content, in (g) ambient conditions, (h) warming, and (i) warming plus snow and N addition. Colors correspond to abundance classes from (a) to (c), height of curves indicate mean species abundance, position on the trait axis indicates mean and SE of trait measurements. Insets (g–i): rank abundance curves for each treatment. While species richness changed very little, increased evenness with rank shifts occurred in (h) and reduced evenness in (i). Experimental site in the moist meadow tundra, Niwot Ridge, Colorado, with a diversity of forbs alongside the abundant bunchgrass (j). See Collins et al. (2022) for more details of the experimental design and modeling framework. Photo credit: Emily Farrer.

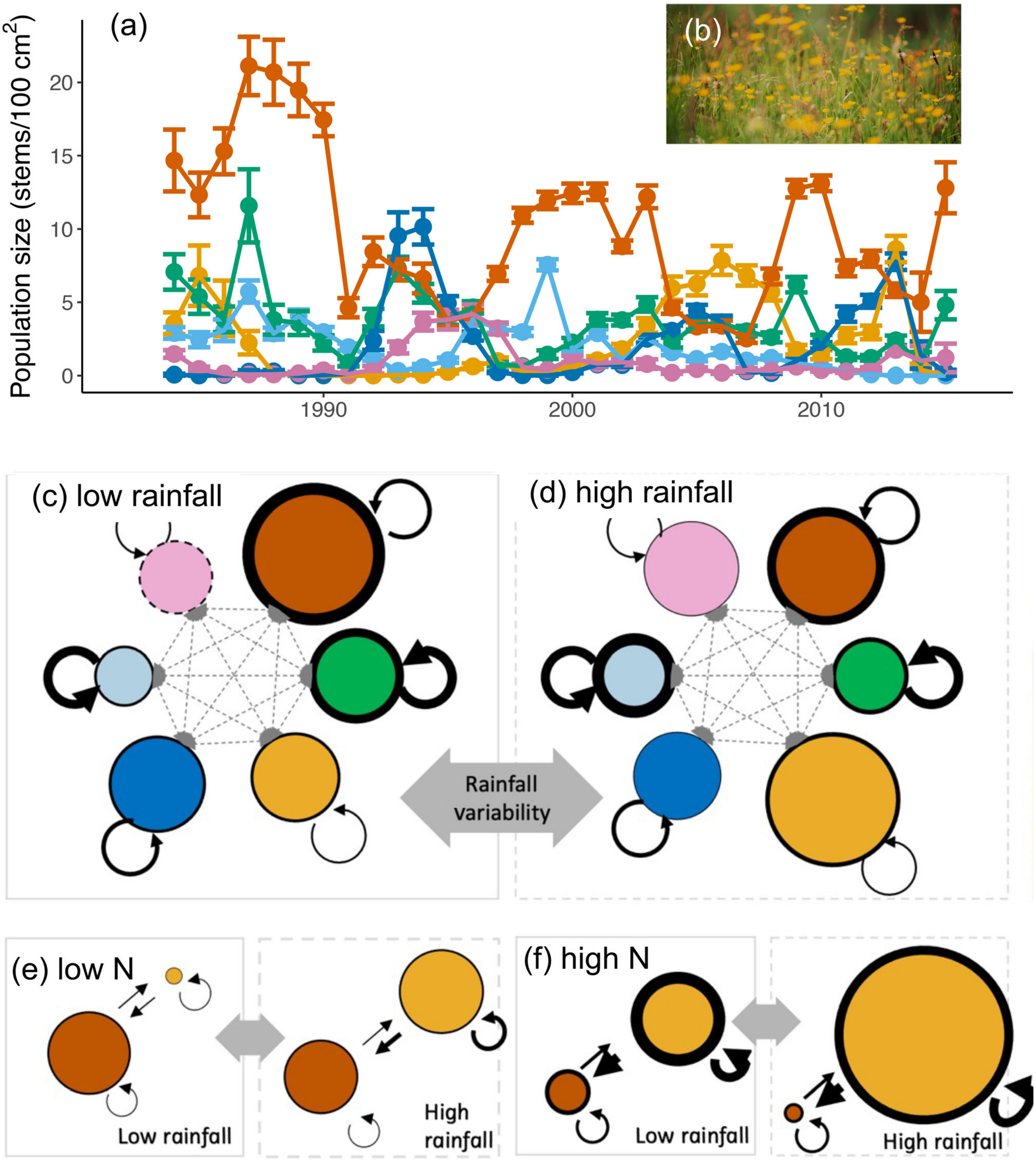

FIGURE 3 An example of frequency control where trade-offs in the intensity of negative density dependence (self-limitation) maintain coexistence in a variable environment. Population size of six common plant species (a): native annual forbs (*Calycadenia multiglandulosa*, light blue; *Lasthenia californica*, green; *Microseris douglasii*, dark blue; *Plantago erecta*, rust), a native annual grass (*Vulpia microstachys*, pink), and a nonnative annual grass (*Bromus hordeaceus*, yellow) fluctuates over time in a serpentine grassland (inset, b). Here we find interspecific interactions (gray dashed arrows) to be weak compared to intraspecific interactions (solid looped arrows). Trade-offs in the strength of conspecific limitation between years with low rainfall (c) and high rainfall (d) maintains diversity. Yet, when the increase in N inputs due to atmospheric deposition are included (e, f), frequency control is overwhelmed by dominance of *Bromus* at high N, with less response to rainfall variability (just *Bromus* and *Plantago* are shown in [e, f] for clarity). Notation follows Figure 2k, with the addition of lambda estimates (growth rate when rare) denoted by the thickness of the line around each species circle. Arrow width indicates strength of intraspecific interactions and circle size indicates relative abundance of species. See Hallett et al. (2018) and Hernandez (2021) for more details of the study design and modeling framework. Photo credit: Lauren Hallett.

regardless of rainfall variability (fig. 3e,f; Hernandez, 2021). Following similar dynamics in the tundra, a shift toward dominance control at high N correspond to trait diversity decline and a shift toward the trait optimum of the competitive dominant *Bromus* species (Hallett, unpublished data).

Positive feedback control in California grasslands at intermediate resource levels

California grasslands can have well-defined patches of both native perennial bunchgrasses and annual exotic grasses (Figure 4a–c). This patchiness persists under some environmental conditions but not others, and global change drivers can push a system both in and out of these conditions (Larios et al., 2013). In a series of "invasion when rare" experiments, combined with demographic modeling along a gradient of atmospheric N deposition (Larios et al., 2017), native perennial grasses (e.g., *Stipa pulchra*, Figure 4b) were the dominant species at low N availability, while at high rates of N deposition, exotic annuals (e.g., *Avena fatua*, Figure 4c) were the superior competitor, suggesting a reordering of competitive hierarchies as the external driver intensified (Figure 4d,f). However, as opposed to cases of dominance control at high or low N, a positive feedback topology occurred at intermediate N inputs (Figure 4e). With intermediate external inputs, internal interactions depended on initial conditions: Native bunchgrasses were competitively superior at high abundance but could not successfully invade when starting from a low abundance (Figure 4h,k). Exotic annuals also exhibited this positive frequency dependence, where they could not invade when rare but could exclude other invaders when abundant (Figure 4h,k).

Many processes can maintain positive feedbacks in nature. In this case, the presence of the native grass *Stipa pulchra* promotes a microbial community that in turn enhances its growth and reproduction (Chung et al., 2019; Larios & Suding, 2015). Feedbacks that maintain the exotic annual grass *Avena fatua* dominance in intermediate environmental conditions do not appear to be microbially mediated but rather maintained by high propagule pressure (Larios et al., 2013).

Application of traits in a system with feedback control is not straightforward, as the traits important in these feedbacks are rarely quantified. Here, the native grass *Stipa* and exotic grass *Avena* vary in traits along the resource axis, as would be expected: *Stipa*, which dominates at low N, is resource conservative, and *Avena*, which dominates at high N levels, has resource acquisitive traits, causing the trait distribution in systems with patches dominated by both to be bimodal (Molinari & D'Antonio, 2014). While we can identify the feedbacks as related to differences in plant–soil interactions (Larios & Suding, 2015), we suspect that the traits that would best predict these feedbacks are different from those we typically measure in a functional trait framework. Expansion of what we consider important traits (e.g., root exudates, immune system, propagule pressure traits) would allow broader inference.

Summary

Across these systems, we illustrate how types of external drivers and internal system topology provide a helpful framework for understanding community reorganization under global change. These factors generalize the complexity of global change and the network of interactions that structure communities. We have inferred external drivers and internal topologies using statistical models that encompass competitive, demographic, and functional dimensions (Collins et al., 2022; Farrer et al., 2014; Hallett et al., 2018, 2019; Larios et al., 2017). Each approach brings important caveats and considerations (Dormann et al., 2017; Feng et al., 2020). Yet, in an era of rapid change where solutions are urgently needed, we hope that the benefits of inference and generalization to highlight useful management interventions outweigh their costs.

APPLICATION TO MANAGEMENT

Planning in restoration and conservation often starts with specific challenges related to changing biodiversity within a system. For example, common management goals may include reducing the abundance of an invading exotic species, bolstering rare or vulnerable species that are in decline, and re-establishing multiple, service-providing native species. Despite the common compositional focus of these goals, the processes underlying these challenges inevitably vary depending on external drivers and internal topologies. Without taking these into account, management efforts may be ineffective at best, and detrimental at worse. For example, in invaded landscapes of the Western United States, restoration seed mixes have historically included species known to have competitive traits (e.g., crested wheatgrass) as a means of reducing dominant invasive species; however, without anticipating the full role of seeded species within internal networks, these efforts have sometimes pushed communities toward a topology that fails to meet management goals (e.g., with low native diversity; reviewed in Davies et al., 2020).

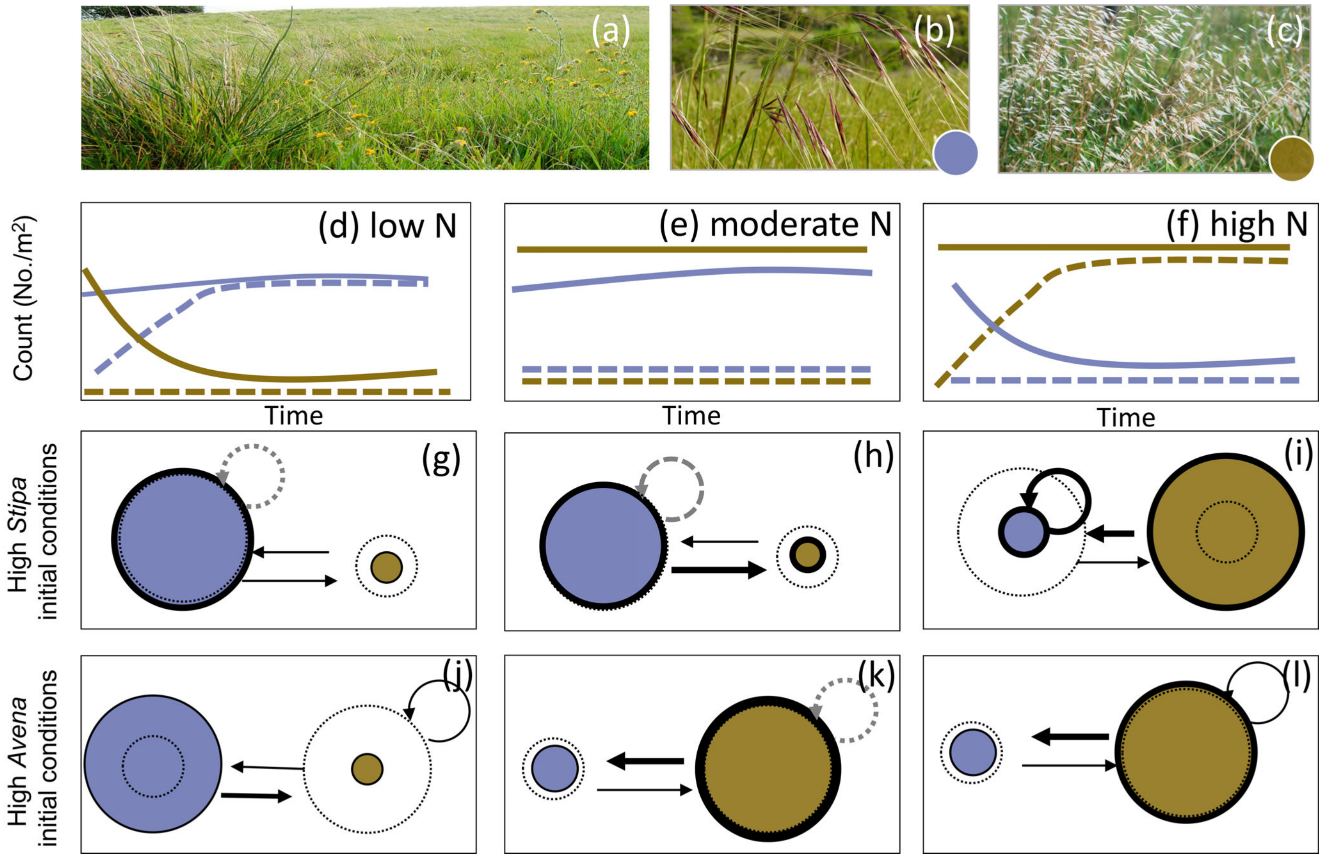

FIGURE 4 Example of positive feedback control in California grasslands (a) where initial conditions (whether the species is abundant or rare) influence long-term abundance patterns. Modeled abundance patterns incorporating demography of a native perennial bunchgrass (purple, *Stipa pulchra* [b]) and an exotic annual grass (brown, *Avena fatua* [c]) across a gradient of soil N levels (d, low; e, moderate; f, high), with dashed lines indicating the "invading" species starting as rare and solid lines indicating the species at high initial conditions. In (d) and (f), long-term abundance patterns do not depend on initial conditions: *Stipa* competitively dominates at low N (g, j) and *Avena* dominates at high N (i, l). At intermediate levels of N (e), the species starting as abundant maintains dominance. The structure of interactions is also affected by initial conditions (native grassland where *Stipa* abundant, g–i; invaded grassland with *Avena* abundant, k–l; initial abundance indicated by size of dashed circle). At intermediate N levels (h and k), the abundant species has positive density dependence and strong asymmetric competitive effects on the rarer species, shifting abundance patterns. Notation follows Figure 2k, with the addition of lambda estimates (growth rate when rare) denoted by the thickness of the line around each species circle. Arrow width indicates strength of intra- and interspecific interactions, with dashed lines indicating positive density dependence, circle size indicating abundance of species group, and dashed circles indicating starting conditions. See Larios et al. (2017) for more details of the study design and modeling framework. Photo credits: Loralee Larios (a), Katharine Suding (b–c).

Here we describe pathways for the EDIT framework to be applied by science–manager teams to both identify the dynamics underlying a management challenge related to global change and evaluate potential solutions. Importantly, while the EDIT framework aims to understand community reorganization in the face of global change, the framework does not assume that one set of dynamics is more or less desirable from a management perspective. Thus, a first step is to identify management goals and desired trajectories of change. Second, science–management partners can work together to combine the necessary data inputs and modeling approaches to implement the EDIT framework. We point to the applied potential of combining modeling approaches with monitoring data sets, functional trait assessments, and experiential knowledge to inform understanding of external drivers and internal topologies in a community. A last step, which we detail in this section, is to determine if interventions are needed and, if so, what they might be. Because the efficacy of an intervention will depend on the external drivers and internal dynamics of the system (Tables 1 and 2), the EDIT framework can be used to evaluate potential solutions to the identified management challenge.

External drivers

Based on the EDIT framework, adjusting system inputs (i.e., critical external drivers) is an effective way to moderate outputs of interest to management (i.e., biodiversity response). Yet, it is often difficult to control external drivers through *local* interventions (Clark et al., 2020; Saavedra et al., 2017). Proximal approaches (e.g., suggestions in Table 1a) often come with impacts that may reduce management efficacy. For instance, to address the dominance of undesirable species that are associated with increased resource availability, grazing could be used to remove excess biomass and nutrients, but it may also cause soil disturbance and selectively remove palatable species that are not the target of management (Fenn et al., 2010; Weiss, 1999). Adding carbon (e.g., in the form of sugar or sawdust) can also be used to reduce soil available N, but the reduction may be transient and costly at scale (Clocchiatti et al., 2023). Likewise, when it is difficult to establish restoration species due to unsuitable abiotic conditions, the introduction of foundational plants can alleviate an abiotic stress, but also affect other species interactions (Losapio & Schob, 2017; Soliveres & Maestre, 2014). Thus, despite the need to address external drivers of global change, local interventions to address the external driver are often difficult. A key decision point may be whether additional or alternative interventions aimed at modifying or supporting the internal network topology can be leveraged (Table 2).

Dominance control

When an external driver shifts a system to a dominance topology, interventions that reduce the abundance or interaction strengths of the dominant species might be required (Funk & Wolf, 2016). For instance, in serpentine systems (Figure 3) that are transitioning from negative frequency control to dominant control with increasing N levels, grazing interventions might target the exotic brome dominating with increased N alongside, efforts to reduce resource inputs. We acknowledge that identifying feasible approaches to selectively reduce the abundance of one species is not trivial. In some cases, like the alpine tundra system where the dominant species is native (Figure 2), increased dominance may not warrant costly intervention. In other systems where a shift toward dominance control may lead to ecosystem transformation, the EDIT framework may help science–manager partners identify intervention strategies like fire, thinning, selective grazing, or herbicide application to reduce the strength of competitive effects and shift the topology away from dominance control.

Facilitative control

Maintaining facilitative topologies requires prioritizing the establishment of particular species that provide refuge for others that may otherwise fail to establish (Soliveres & Maestre, 2014; Thomsen et al., 2010). The EDIT framework could help identify thresholds for nurse plant densities that optimize positive interactions (e.g., Brigham & Suding, 2023).

Negative frequency control

Maintaining networks with strong negative frequency dependence requires a focus on functional diversity and maintenance of complementary species (niche breadth). These types of interventions may best focus on maintaining and perhaps even creating environmental (abiotic and biotic) heterogeneity (Hallett et al., 2017; Stein et al., 2016). In frequency control topologies, removal of undesirable species may be most effective when the species' growth rate is depressed. For instance, removal efforts should coincide with low population growth rates of the invader in a serpentine system (*Bromus*, Figure 3) due to its rainfall sensitivity (Hallett et al., 2018).

Positive feedback control

Positive feedback topologies can be resilient to changing environmental conditions due to the strength of internal feedbacks. Yet, once the environment changes past a certain threshold, abiotic effects can overwhelm internal feedbacks and lead to rapid change (Dudney & Suding, 2020). Thus, managers might expect longer periods of stasis and increased risk of abrupt changes under extreme environmental conditions (Turner et al., 2020). These systems also require increased attention to initial conditions and legacies, as needed interventions may differ depending on what species dominates initially, and through what type of feedback (Godoy, 2019). For instance, protection of intact *Stipa* grasslands (Figure 4) at intermediate N levels is a priority. Breaking feedbacks related to undesirable forms of resilience (e.g., those created by invasive species) might need to combine a removal of legacies with the introduction of new, adapted species that shift priority effects (Cleland et al., 2015; Schantz et al., 2015). Restoration of exotic *Avena* grasslands, for instance, may best target native forbs rather than *Stipa* at higher N levels (Larios et al., 2017).

Summary

A core guiding concept across the EDIT framing is that efficacious intervention depends on understanding the dynamics causing biodiversity change (e.g., external drivers, internal topology) rather than patterns in species richness or rank abundances alone (Bergstrom et al., 2021; Lindenmayer & Likens, 2010). Opportunities to address external drivers at the local scale may be limited, given global phenomena, and local intervention more often suited to address internal dynamics in the context of global change. Understanding the available options is key, and these options fundamentally depend on an understanding of how community reorganization is occurring in the context of global change.

CONCLUSIONS

Continued demands on nature, combined with changing global conditions, will cause substantial shifts in biodiversity during our lifetimes. Some of these changes will be irreversible. Actions to lessen the impact of external drivers of global change (e.g., climate mitigation, pollution reduction, land protection) are necessary but not sufficient to prevent future biodiversity declines. By considering community reorganization as a key component of local diversity change that is driven by external drivers and how these drivers modulate internal dynamics, EDIT can provide a template to guide future biodiversity trajectories that ideally benefit nature and society. We argue here for a balance between a mechanistic, quantitative understanding utilizing models of external and internal dynamics of change and generalizable approaches that can fuel practical inference with available compositional monitoring and functional trait data sets. We hope to have demonstrated how these approaches can be used to diagnose which EDIT components are operating within a given system and how this insight can be used to guide efforts to manage community reorganization through time.

As we expand from traditional diversity measures to consider external drivers and internal controls on community reorganization, establishing dynamic goals, such as ensuring that systems can adapt to and track global environmental change, will be increasingly possible. These goals are already in use qualitatively, with policymakers often using terms such as ecological integrity (Donohue et al., 2016; Lajeunesse et al., 1995; Suding et al., 2015), self-sustainability (Palmer et al., 2014), and ecosystem health (Díaz et al., 2015). Quantitative metrics based on how external drivers modulate internal topology can bridge these qualitative constructs. However, this is new territory, particularly for terrestrial plant–plant interactions, with many unanswered questions: Do these topologies represent distinct, nonrandom states, or is it better to describe community topologies as a gradient of many types of interactions? How do transient and lagged responses in topologies affect our power of inference? By narrowly defining community topologies, do we overlook important complexity (e.g., multilayer networks) that drives community responses to global change?

While imperfect, multiple modes of inference are essential to make informed, purposeful choices about how to respond to community reorganization due to global environmental change (Beaury et al., 2020; Dudney et al., 2022). Institutional support that includes "safe-to-fail" actions and experimentation is key to empowering managers to make innovative decisions that go beyond reactive triage (Aplet & McKinley, 2017). Management interventions, particularly in combination with monitoring, can also test our scientific inference in a decision-making space (e.g., the resist–accept–direct framework; Lynch et al., 2021) and increase adaptive capacity (Dudney et al., 2022). In the face of uncertainty under global change, bidirectional exchange between scientists and managers will best refine this framework and inform on-the-ground management interventions.

Lastly, placing the external drivers and internal topologies into a few baskets is a clear oversimplification. Certainly, different systems may vary in the types of external threats they experience and how they are internally organized in network structure, and our narrow focus on plant–plant interactions in terrestrial plant communities misses important taxa, interaction types, and multilayer networks (Pellissier et al., 2018; Pilosof et al., 2017). As disturbance can initiate new assembly (DeSiervo et al., 2023; Kopecky et al., 2023), another key unknown is whether management intervention during a period of disassembly may be an effective precursor to guide reassembly toward a desired trajectory of reorganization (Perez-Navarro et al., 2021; Seidl & Turner, 2022).

Even at the broadest level, the drivers and topologies we suggest should be considered hypotheses for testing and refinement. In these times when progress is urgently needed, however, we hope that they offer heuristic value in thinking about the connection between different ecological theories of change and how these theories can provide managers a template to guide opportunities for intervention.

AUTHOR CONTRIBUTIONS

Katharine N. Suding conceived of and led the writing of the manuscript. Courtney G. Collins, Lauren M. Hallett, and Loralee Larios contributed data that were essential in figure creation. All authors contributed critically to the ideas and writing and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

We include three previously published case studies with data sets available as follows: alpine tundra data (Collins, 2022) in Zenodo at https://doi.org/10.5281/zenodo.6599883; serpentine data (Hallett et al., 2020) in the Environmental Data Initiative Data Portal at https://doi.org/10.6073/pasta/b34798fd71e24efd3fda995ec4263701; California gras slands data (Larios et al., 2018) in Dryad at https://doi.org/10.5061/dryad.7qj20.

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