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OPINION ARTICLE

Leveraging nature's backup plans to incorporate interspecific interactions and resilience into restoration

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Interspecific interactions are important structuring forces in ecological communities. Interactions can be disturbed when species are lost from a community. When interactions result in fitness gains for at least one participating organism, that organism may experience reduced fitness as a result of interaction disturbance. However, many species exhibit traits that enable individuals to persist and reproduce in spite of such disruptions, resulting in resilience to interaction disturbance. Such traits can result in interaction generalization, phenotypic and behavioral plasticity, and adaptive capacity. We discuss examples of these traits and use case studies to illustrate how restoration practitioners can use a trait-based approach to examine species of concern, identify traits that are associated with interspecific interactions and are relevant to resilience, and target such traits in restoration. Restoration activities that bolster interaction resilience could include, for example, reintroducing or supporting specific functional groups or managing abiotic conditions to reduce interaction dependence by at-risk species (e.g. providing structural complexity offering shelter and cover). Resilience may also be an important consideration in species selection for restoration. Establishment of resilient species, able to persist after interaction disturbance, may be essential to restoring to a functioning ecological community. Once such species are present, they could help support more specialized species that lack resilience traits, such as many species of concern. Understanding the conditions under which processes linked to resilience may enable species to persist and communities to reform following interaction disturbance is a key application of community ecology to ecological restoration.

Key words: generality, interaction disturbance, mutualism, plasticity, traits

Implications for Practice

- Many species display traits that confer generalization, plasticity, or adaptive capacity, making them resilient to disruption of key interactions upon which they depend.
- Identification of such traits in restoration planning, using the decision tree provided here, can enable restoration activities to take advantage of and leverage these traits.
- Planning for interaction recovery and improved resilience should increase restoration efficiency and effectiveness.

Introduction

Interaction disturbance, a specific class of ecological disturbance, refers to the disruption of interactions between a given set of species (Brodie et al. 2009; Aizen et al. 2012). Such disturbances can be disruptive to both partners and the communities in which they are embedded. Many organisms, however, exhibit traits that confer reduced dependence on interaction partners. These traits may increase resilience in the face of interaction disturbance: that is they may boost the probability that populations or processes persist following disturbance (in effect, absorbing the disturbance) (Holling 1973) (Fig. 1). As an example, certain Central American plants with hard, large seeds were likely dispersed by now-extinct Pleistocene megafauna (Janzen & Martin 1982), and extinction of such megafauna left no potential dispersers among the native fauna, resulting in seed dispersal disruption for these species. The introduction of livestock to Central America has inadvertently restored the function of seed dispersal for these species because the seeds are able to be dispersed by non-native livestock in addition to their historical dispersers (Janzen & Martin 1982). Fruit and seed traits attracting livestock thus confer resilience to interaction disruption for those species. In ecological restoration, recognizing factors contributing to resilience may enable practitioners to identify species and processes that are poised to recover from

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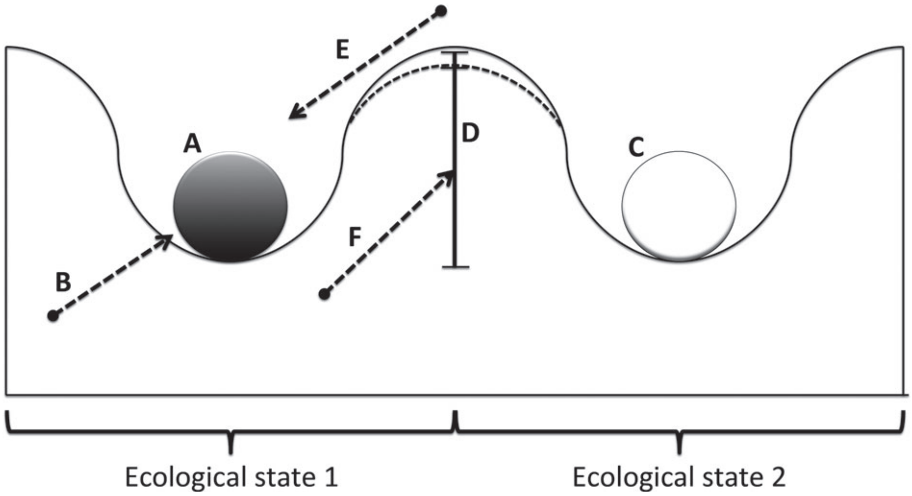

Figure 1. Conceptual model of the relationship between interaction disturbance, resilience, and restoration. A given system originates in ecological state 1, represented by the position of the ball in the diagram as (A). Interaction disturbance (B), by altering the populations and processes in the ecosystem, can propel the system into a new ecological state (C). Traits of the species involved in the interaction can dictate the resilience of the interaction (represented as the height of the hill, D), or how likely it is to return to its former state following the disturbance. Community-level restoration can work to return the system to its previous state via pressure exerted across the system trajectory (E). Individual-level restoration can leverage traits to boost inherent resilience factors (F), thus in effect elevating the height of (D).

interaction disturbance versus those that will remain in a new state, with the potential to alter the broader systems in which they occur (Biggs et al. 2012; Lake 2013; Alday & Marrs 2014) (Fig. 2). Resilience pathways may then be leveraged or bolstered in restoration planning.

Disturbance of interactions is distinct from disturbance of ecosystems or full communities, although interaction disturbance may cascade up to these higher levels. An awareness of this distinction is important for restoration incorporating resilience theory (Fig. 3). Community-scale disturbance often affects sites that have experienced some sort of natural or anthropogenic physical disturbance, such as a fire, flood, treefall, mine, and so on. Disturbance of interactions, however, is often more subtle. Overhunting that removes large predators or seed dispersers while leaving most other species undisturbed is an example (Terborgh et al. 2008; Estes et al. 2011). In such circumstances, disturbed interactions appear likely to alter species assemblages over time (Terborgh et al. 2008) and could impact communities by, for example, resulting in dominance by different taxonomic and functional groups in systems lacking interactions versus intact systems (Tabarelli et al. 2010). In this way, disturbance that impacts interactions may alter networks of interacting communities, impacting population sizes and eventually biodiversity (Redford 1992). Interaction network analysis allows visualization and analysis of these dynamics, indicating which species interact and with what frequency (Bascompte & Jordano 2013). Through network analysis, it has become clear that interaction networks are often highly nested, wherein specialized species (i.e. those that interact with a single or very small number of partners) interact with generalized species (i.e. those that interact with large numbers of partners), a dynamic that confers stability to the network (e.g. Verdú & Valiente-Banuet 2008). Losses of particular species can alter the interactions between others, a process known as rewiring (Ramos-Jiliberto et al. 2012), with the potential to impact other species in a variety of ways.

An understanding of the importance of species interactions is becoming a central part of modern restoration ecology (Holl et al. 2000; Young et al. 2005). Techniques for on-the-ground application of this understanding are currently emerging (Fraser et al. 2015). Certain traits may make populations and processes less vulnerable to interaction disruption, whereas populations of species that lack these traits may be more at risk and could be placed on extinction trajectories as a result of interaction disturbance (Valiente-Banuet et al. 2015). Active restoration may be necessary for such at-risk species. We discuss some of the key traits that may result in resilience of populations and processes to interaction disturbance, illustrating the relevance of such traits with examples from a wide diversity of systems and taxonomic groups. We provide case examples of restoration work that take into account interaction disturbance and relevant species traits, demonstrating the capacity of practitioners to leverage these traits to effectively restore populations and processes. Finally, we discuss steps to integrate interactions and resilience to interaction disturbance into restoration planning. We provide a decision tree to guide readers through this process (Fig. 2), and translate these community ecology and resilience concepts to active restoration decision making (Fig. 3).

Species Traits Related to Interaction Disturbance Resilience

Traits related to generalization, plasticity, and adaptive capacity may contribute to interaction disturbance resilience. Generalization occurs when species are capable of interacting with a variety of partners that are at least somewhat functionally redundant

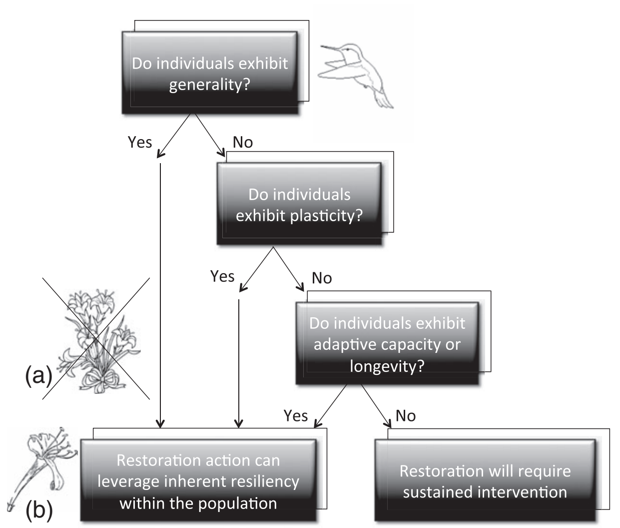

Figure 2. Decision tree guiding restoration practitioners through the process of recognizing when a target species exhibits traits that may confer inherent resilience to the effects of interaction disturbance. When it seems likely that inherent resilience is present, restoration practitioners can work to leverage and support that resilience, supporting existing ecological processes likely to return populations to their pre-disturbance state. However, when traits that confer resilience to interaction disturbance are lacking, the target species may only persist in the face of disturbance if its populations are actively and continually supported by conservation effort. We illustrate this decision tree with a simple example: loss of riparian vegetation in the central Sonoran Desert has decreased the relative availability of hummingbird plants (a), possibly contributing to nest failures in some regions (S. Wethington 2012, Hummingbird Monitoring Network, Patagonia, AZ, U.S.A., personal communication). However, hummingbirds are generalist feeders, able to obtain nectar from a diversity of potential plant species rather than from a single or limited suite of partners. Restoration that includes planting of tubular, nectar-providing flowers (b), even as substitutes for species no longer available, is likely to assist hummingbird population persistence, taking advantage of the hummingbirds' generality and inherent resilience to losses of particular nectar plant species.

(i.e. they do not depend on a single partner due, e.g. to traits emerging from coevolution with that partner). Phenotypic plasticity, or variability in morphology or behavior, can confer generalization by allowing species to partner-switch or can enable species to persist in the complete absence of interactions. Adaptive capacity, the underlying genetic variation allowing for relatively rapid evolutionary response, may enable species to evolve the traits required to persist following interaction disturbance. We explore each of these mechanisms of resilience below.

Species interactions are often generalized. If some partner species are lost via interaction disturbance, species able to interact with many partners should be less affected than species reliant upon more specialized associations. Importantly, the quality of mutualistic interaction can vary among partners, so the loss of some of its partners may still impact a given focal species. The level to which generalization confers resilience to interaction disturbance will therefore depend on which species are lost and the characteristics of the remaining interactions.

Generalization is evident in a diversity of interaction types. In many commensal interactions, for example, one species may use any of a broad suite of potential partners for protection from harsh conditions (e.g. nurse–plant relationships; Aparicio et al. 2004) or from predation (e.g. camouflage decoration in the decorator crab *Libinia dubia*) (Stachowicz & Hay 2000). In mutualisms, floral traits such as wide, open flowers can permit plants to be pollinated by a wide diversity of species (Bosch et al. 1997). Small fruits or seeds that can be swallowed by animals with varying gape widths foster seed dispersal by a diversity of potential partners (McConkey & Drake 2002). In protection mutualisms, production of unspecialized rewards can lead to large assemblages of potential defenders (e.g. Ness et al. 2006), assuring protection even after loss of a specific partner; examples include ant-plant (Guimarães et al. 2006) and sea anemone-fish mutualisms (Ollerton et al. 2007). Traits such as generalist root morphology and mycorrhizal structure may result in diverse plant and fungal partners within mycorrhizal relationships, protecting both sides from mutualism disruption (Moora et al. 2011).

Many predators, herbivores, or parasites can opportunistically use a variety of potential food items or host species. For example, the California condor (*Gymnogyps californianus*) likely once relied on now-extinct Pleistocene megafauna, but now consumes livestock carcasses as a substantial portion of its diet (Chamberlain et al. 2005). In urban areas of California, where native plants are scarce, native butterflies utilize non-native host plants (Shapiro 2002); if this change enables persistence of the butterflies over time in the face of disturbance of their historic interactions, then such generality has, by our definition, conferred resilience on butterfly populations.

Phenotypic plasticity can also reduce dependence on a particular interaction partner, enabling a species to shift from one partner to another as relative availability of partners fluctuates. Thus, plasticity may allow sequential shift between partners. The sunfish *Lepomis humilis* exhibits variable morphology depending on the identity of arthropod prey present during the fish's juvenile development, potentially permitting it to more efficiently consume whatever prey is likely to be available later in its life (Hegrenes 2001). Barnacles exhibit longer-feeding structures in more protected sites, permitting increased prey capture where water flow is reduced (Marchinko 2003). Behaviorally, prey switching could entail plasticity, for example, when it has involved shifts between diurnal and nocturnal feeding in some fish (Reebs 2002) and mammals (e.g. Pereira 2010), and from terrestrial to arboreal habitats in tiger snakes (*Notechis scutatus*) (e.g. Aubret & Shine 2008).

Plasticity may enable interactions to persist even when availability of mutualists varies. The orchid *Satyrium longicauda* produces larger inflorescences when pollinators are scarce, increasing inflorescence attractiveness (Harder & Johnson 2005). The coral *Acropora millepora* hosts various species of symbiotic zooxanthellae in its tissues, but the dominant symbiont varies according to external environmental cues, leading to different partnerships in warmer versus cooler water (Berkelmans & van Oppen 2006). The pollen of some plant species can be transferred by wind or water in addition to animals

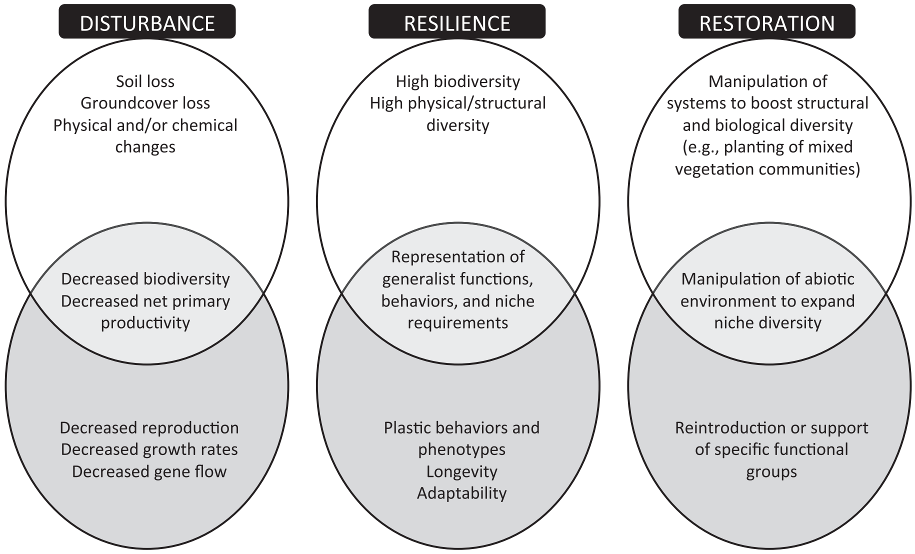

Figure 3. Relationship between community-level (white circles) and interaction-level (gray circles) disturbance effects, resilience factors, and restoration responses. Overlap between the circles indicates elements common to both community-level and interaction-level restoration (e.g. the presence of generalist species may help to restore both community-level and interaction-level functions).

(e.g. Bernhardt et al. 2003). Many outcrossing plants are able to reproduce by budding, clonal growth, or self-fertilization (Holsinger 2000; Barringer 2007). Similarly, wind, water, and gravity dispersal can reduce the dependence of some plant species on seed-dispersing mutualists (Imbert & Ronce 2001).

Plant species that interact commensally with protective nurse plants may be able to survive without a partner, for example, by utilizing rock crevices for shelter (Peters et al. 2008). Animals that use commensals for cover in extreme temperatures may instead move underground during hot periods (Bortolus et al. 2002). Species such as chameleons (family, Chamaeleonidae) can alter their coloration to blend in with rocks or other substrate in response to a change in plant species (Stuart-Fox & Moussalli 2009).

Adaptive capacity may enable species to cope with interactions that are unpredictable over time by evolving new mechanisms that allow them to persist following interaction disturbance (Kiers et al. 2010). For example, decorator crabs have been shown to select different camouflage algae depending on the environment in which they are found as a result of evolutionary divergence between populations (Stachowicz & Hay 2000). Populations of the paperwhite, *Narcissus papyraceus*, display different floral traits in different locations, consistent with preferences of local pollinators (Pérez-Barrales et al. 2007). Loss of large-bodied seed dispersers in Brazilian rain forests has resulted in rapid selection for smaller fruit size in palms (Galetti et al. 2013). Similarly, genetically-based differences in host plant preference have arisen in herbivore populations following changes in host plant availability (Singer & McBride 2010).

Like plasticity, evolution of new traits can sometimes permit organisms to persist without interaction partners. Self-compatibility, for example, has evolved within lineages that were formerly obligately outcrossing, as in the case of *Aster furcatus* (Reinartz & Les 1994). In some cases, evolutionary changes such as these have occurred remarkably quickly (e.g. within 30 years for *Spartina*; Sloop et al. 2009).

Of course, there is likely a phylogenetic signal in many of the traits discussed here. Traits that confer generalization, for example, may be common to many of the species in a given lineage (Gómez et al. 2010). If traits related to resilience are identified for particular species, other closely related species may also exhibit such traits and could thus be similarly important in restoration planning.

The Role of Interactions and Resilience in Restoration: Case Studies

We have briefly explored traits linked to resilience following interaction disturbance. We now bring this information into the real world of restoration by very briefly describing two case studies wherein resilience of interactions was fundamental to restoration success. Although differing in ecosystem type and source of disturbance, these illustrate the importance of interactions to restoration. Furthermore, in each of these cases, the interaction disturbance was significant and a straightforward restoration to historical conditions is not possible. Restoration efforts in one of these cases supported a shift to new partners when historical partners were extinct and in the other case supported persistence of native species in partial absence of partners by manipulation of the abiotic environment. Species traits linked to resilience enabled them to persist under such changed conditions and bolstered the success of the restoration efforts.

Endemic Hawaiian Lobeliads

Several of the endemic Hawaiian lobeliad plant species (family, Campanulaceae) are critically endangered as a result of browsing by non-native species and widespread pollinator extinction (van Riper et al. 1986). Efforts to restore lobeliad populations and native plant communities include outplanting into forest sites fenced to exclude exotic browsing mammals (R. Robichaux 2014, University of Arizona, Tucson, AZ, U.S.A., personal communication). Outplanting of lobeliads at high-elevation sites with maximum diversity of remnant native as well as non-native nectarivorous birds boosts redundancy in the pollinator guild and elevates the probability of pollination (Aslan et al. 2014). Protection of remnant lobeliads from non-native mammals enhances the structural diversity of forest patches. In this system, therefore, restoration efforts have taken advantage of the generality and plasticity of the focal plants (i.e. their ability to partner with multiple pollinator species and to grow across a wide elevational range) to directly ameliorate interaction disturbance and to boost resilience.

Traits relevant to lobeliad restoration efforts: ability to partner with multiple pollinators (generalization) and ability to grow at multiple elevations (phenotypic plasticity).

Coral Reef Restoration

In coral reefs, two key guilds of interaction partners are those that promote coral colonization and those that graze on macroalgae, which outcompete young corals (Fitz et al. 1983; Wittenberg & Hunte 1992; Breitburg 1998). Given the importance of grazing fish in reducing algal competitors for coral recruits, rebuilding redundancy in the grazer guild (i.e. restoring multiple species that engage in grazing interactions) is an essential component of coral reef restoration. Such restoration thus takes into account generalization—by having multiple species within a particular functional group—in active coral reef restoration efforts.

Complex physical structures are also relevant to reef restoration. Climate change and coral bleaching (which occurs due to disrupted interspecific interactions within the corals themselves) threaten coral reef ecosystem health (Hughes et al. 2003). Complexity of the physical habitat boosts coral reef resistance to bleaching (West & Salm 2003). Phenotypic plasticity of corals can boost such complexity. Restoration activities may thus include construction of habitat features that provide protection and take advantage of the phenotypic plasticity of reef species by inclusion of either corals with varying architectures or complex and varying artificial substrates in reef restorations.

Traits relevant to coral reef restoration efforts: ability to obtain key-grazing services from multiple fish species (generalization) and ability to obtain protection from diverse substrates and materials (phenotypic plasticity).

Practical Restoration of Interactions, Leveraging Inherent Resilience

Populations and processes that are resilient will tend to return to their previous function following disturbance of interactions, whereas those that exhibit less resilience may be propelled into alternative stable states by interaction disturbance (Fig. 1). The first step in interaction restoration must be identifying interactions in which species at risk participate and determining whether such species exhibit traits that might confer inherent resilience to interaction disturbance. This goes beyond simply knowing the species and its basic needs. For example, rather than just identifying interactions the species participates in, this requires understanding if there is a possibility for the species to persist without those interactions or to switch to new partners and how to facilitate such shifts. This may require research on species of interest (e.g. to determine whether a bat-pollinated plant can also receive pollination from insects if bats are no longer present). Thus, a deeper understanding of how a given interaction functions for a target species becomes necessary. For each such species, a specific series of questions examining relevant traits can be applied, guiding practitioners through a decision tree that identifies these traits for restoration planning (Fig. 2). The next step is to identify specific strategies that take advantage of those resilience traits to improve restoration following disturbance of interactions (Fig. 3). State-and-transition models permit desired conditions and potential pathways to achieve them to be identified (Wilkinson et al. 2005). Restoration efforts can, for example, maintain diverse successional states across landscapes (Bengtsson et al. 2003) or reintroduce specific functional groups such as pollinator-supporting plants (Fig. 3; Wilkerson et al. 2014). Active community-scale restoration prioritizes structurally complex habitats and diverse species assemblages (Fischer et al. 2006). For interaction disturbance, the same principles suggest that restoration activities that create complex habitats could provide the necessary substrate for diverse interactions (Fig. 3). Restoration activities informed by resilience theory can engineer habitats and introduce species with an eye to interaction recovery. This process has the potential to boost overall ecosystem function.

Once species with resilience traits are established via restoration practices, network characteristics such as nestedness suggest that those species, with their tendency to interact with many partners, could form the backbone of a broader community of interactors that could also include more specialized species. Thus, the concepts discussed here may provide guidance to species selection in restoration plantings and introductions. Beginning with resilient species could permit ecological functions to continue following interaction disturbance and, at the same time, provide the interaction substrate upon which a more diverse community can establish.

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