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OPINION ARTICLE

A call for applying trophic structure in ecological restoration

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Ecological restoration projects have traditionally focused on vegetation as both a means (seeding, planting, and substrate amendments) and ends (success based upon primary productivity and vegetation diversity). This vegetation-centric approach to ecological restoration stems from an historic emphasis on esthetics and cost but provides a limited measure of total ecosystem functioning and overlooks alternative ways to achieve current and future restoration targets. We advocate a shift to planning beyond the plant community and toward the physical and biological components necessary to initiate autogenic recovery, then guiding this process through the timely introduction of top predators and environmental modifications such as soil amendments and physical structures for animal nesting and refugia.

Key words: ecological restoration, ecosystem reclamation, food web theory, industrial disturbance, trophic cascade

Implication for Practice

- Ecosystem restoration projects are goal-oriented, but these goals are too often focused on plant productivity and plant species diversity.
- Functioning food webs are a productive goal for restoration projects, yielding recovery of ecosystem functions in addition to plant diversity.
- Research is needed to determine how decomposers, herbivores, and predators affect plant diversity and total ecosystem function.
- Understanding site-specific food webs at the onset of degradation is key to successful restoration.

Introduction

A heightened appreciation for ecological restoration stems from increasing public awareness of how human impacts on the environment negatively affect human health (Chivian 2002), economic well-being (Costanza et al. 1997), biodiversity (WWF 2014) and standards of living (Nisbet et al. 2008). As a consequence, legislation in many nations requires the mitigation and restoration of ecosystems damaged by deliberate human activity (Brandon 2013). To that end, industry-specific regulations have been developed for a number of industries such as mining, oil and gas, forestry and transportation (Tordoff et al. 2000; Visseren-Hamakers & Glasbergen 2007). At the same time, increased global demand for natural resources, and the inevitable habitat destruction that accompanies resource extraction calls for more and better restoration efforts.

Bradshaw (1987) stated that our ability to restore a system is a litmus test of our core understanding of that system's ecology; if we are unable to restore an ecosystem with certainty, it is unlikely that we understand it sufficiently. Historically, land restoration efforts had the primary goal of re-establishing vegetation, but this narrow view can limit ecosystem development, and can result in restoration failure (Fagan et al. 2008; Simmers & Galatowitsch 2010). We argue instead that restoration efforts should include the goals of developing food web structure, increasing biodiversity and enhancing ecosystem services. Restoration practices focused on these outcomes will necessarily lead to an ecosystem-based approach to restoration that is preferable to a vegetation-centered approach because a community with diverse multi-trophic species with high trophic transfer

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efficiency is more resilient and self-sustaining (Dobson et al. 2009; Filotas et al. 2010). We add our voices to the growing chorus that in light of our understanding about how ecosystems structure and function, the incorporation of trophic structure in restoration is essential (Palmer et al. 1997; Vander Zanden et al. 2006; Lake et al. 2007; Dobson et al. 2009; Pillai et al. 2011; Montoya et al. 2013).

Restoration of animal communities seems to mostly follow the "Field of Dreams" hypothesis: "if you build it, they will come" (Palmer et al. 1997, 2010). This laissez-faire approach to ecosystem restoration applies the outdated notion that ecosystems are controlled only by bottom-up processes where plants provide the energy and nutrients that support animals in higher trophic levels. This view ignores the growing scientific understanding that feedbacks from animals can cause top-down control that determines the abundance and diversity of plants as well the rate at which nutrients are cycled through ecosystems (Bardgett & Wardle 2010; Schmitz et al. 2010). There is also a large body of work on the relationship between the non-random structure of species interactions, within and between trophic levels, and community stability (May 1972; Pimm 1984; McCann 2000; Thébault & Fontaine 2010; Allesina & Tang 2012; Mougi & Kondoh 2012; Loreau & de Mazancourt 2013; Sauve et al. 2014). Hence, if the ultimate goal of restoration is recovery of self-sustainable, stable, and resilient communities, the re-establishment of top-down and bottom-up controls, and ecological networks must be planned. We argue that this approach requires more explicit emphasis on targeting the species compositions of food webs comprising ecosystems and their interactions.

Application of Food Web Theory to Restoration

Food web theory is an essential tool for restoration ecology because of its intersection with population, community, and ecosystem ecology. Current food web theory incorporates both top-down and bottom-up processes because both occur simultaneously (Turkington 2009; Strong & Frank 2010; Terborgh & Estes 2010; Thompson et al. 2012). In addition, applying concepts such as ecological networks, trophic cascades, food web stability, and diversity–ecosystem function relationships offers a richer way to consider the functioning of each system in terms of top-down (consumer control) and bottom-up (resource control) forces, and ecological networks (Loreau & de Mazancourt 2013; Sauve et al. 2014). Few of these concepts are ever utilized in restoration practice, even though they are sometimes addressed in the restoration literature (Palmer et al. 1997; Vander Zanden et al. 2006). The challenge in applying them lies in differentiating the ecological conditions in which bottom-up and top-down control predominate, trophic cascades occur, and ecological networks confer stability.

Productivity can influence trophic structure and ecological networks. An interesting intersection between terrestrial and aquatic systems is leaf litter inputs into streams. Leaf litter is a major carbon pathway and is important in stream systems (Webster & Meyer 1997). Wallace et al. (1997) experimentally excluded leaf litter from a headwater stream for 3 years, and found declines in most invertebrate taxa, which are a food source for multiple predators in stream and on land (Power & Dietrich 2002). Stream restoration must therefore consider inputs of terrestrial/riparian detritus for successful food web recovery.

Trophic cascades can affect productivity. The trophic cascade hypothesis proposes that feeding by piscivores and planktivores affects rates of primary production in lakes such that there is a top-down influence of predators on prey through multiple trophic levels (Carpenter et al. 1985). A good example in a terrestrial system is the effect that certain hunting spider species exert on plant productivity in old fields (Schmitz 2003). Schmitz compared productivity and community composition in systems with just plants, plants with insect herbivores, and plants with insect herbivores and spiders. Plant productivity increased as a function of both herbivore and predator removal, because predators drove herbivores to predation refuges dominated by highly productive plant species. By feeding on these plants, herbivores suppress productivity but also promote plant species evenness, because subordinate plant species were released from competition. Another example of predator–prey interactions influencing productivity involves the predatory interaction of a beetle (*Agonum impressum*) on earthworms. Theory suggests that predators consuming earthworms will negatively impact primary production by limiting aeration and essential nutrient mineralization in soils. By contrast, Zhao et al. (2013) found that beetles drive earthworms to deeper soil strata while having a relatively small impact on earthworm population density. This non-consumptive predator effect led to improvements in soil structure and development and consequently augmented primary production.

As biodiversity increases and food webs develop, ecosystem complexity increases and, generally, so does ecosystem stability (Lake et al. 2007; Rey Benayas et al. 2009; Filotas et al. 2010). Plant community diversity is often correlated with diversity of higher trophic levels (Haddad et al. 2009) which in turn is purported to impart resilience to adversity (e.g. drought) (Frank & McNaughton 1991; Bloor & Bardgett 2012) and to facilitate ecosystem processes (Naeem et al. 1994). This evidence supports a strong argument to aim for high plant diversity in restoration projects. By contrast, few studies have addressed higher trophic level diversity or its effects on resources. Otto et al. (2008) evaluated the effects of predator diversity on herbivore survival and primary producer biomass in a tri-trophic system. They tested whether consumer additivity, identity, or compensation predicted cascading outcomes at lower trophic levels. They discovered that predator identity and phenology played significant roles in determining the strength of trophic interactions. This example reveals the need to determine not only the processes governing intratrophic organization, but also how similar or contrasting processes interact at multiple trophic levels. Testing analogous concepts at multiple trophic levels provides an opportunity to determine the generality of various resource and community theories within a single interacting system, and to better understand their dynamics.

Many animal species naturally recolonize restored habitats (e.g. Cristescu et al. 2013) and restoration ecology increasingly promotes species introductions and leaving space and habitats for natural colonization (Choi 2004; Hendrychová et al. 2012; Grégoire Taillefer & Wheeler 2013). Several bird species showed marked increases in abundance after vegetation had been re-established in a riparian corridor in Iowa (Benson et al. 2006). Some riparian restoration efforts may be aimed at conserving particular animal species of concern, which depend upon provision of specific host plants (Rood et al. 2003).

Small mammals on the forest floor show variable responses to clearcutting with generalist species persisting and specialist species disappearing. The abundances of mammalian carnivores are also reduced by clearcutting because of the loss of preferred prey species, den sites, and other components of forest stand structure (Fisher & Wilkinson 2005). Motivated by this observation, Sullivan et al. (2012) posed the question: if we build habitat with woody debris structures on clearcuts, will forest mammals come? Coarse woody debris provides many important functions that are essential to maintaining biodiversity and long-term ecosystem productivity. In commercial forests, woody debris is the residue (slash) left after conventional and salvage harvesting. Woody debris structured as piles and windrows were compared with the typical dispersed distribution of debris for use by a specialist small mammal, the southern red-backed vole (*Myodes gapperi*) and two mammalian carnivores: the short-tailed weasel (*Mustela erminea*) and the American marten (*Martes americana*). Three years of sampling indicated that mean abundance of red-backed voles differed among the treatments with the highest counts in windrows and the lowest in the dispersed treatment. Total abundance and species richness of small mammals was highest in piles and windrows. As a complement to restoration practices, adding non-living structures as nesting and refugia in land reclamation following mine closure could be a useful tool for the reintroduction of animals.

Restoration can involve the removal of non-native species. Non-native predators in temperate lakes have caused large declines in native fish communities and alterations of trophic structure (Vander Zanden & Rasmussen 1999). When a non-native apex predator (smallmouth bass) was removed from a temperate lake, a stable isotope analysis revealed that the native apex predator (lake trout) increased their trophic position within 2 years (Lepak et al. 2006).

These examples underline the need for a synthetic, multi-trophic approach to restoration, and highlight some of the basic research necessary to determine when and how to introduce carnivores and herbivores to a recovering ecosystem. Success with wolves in Yellowstone National Park (Kauffman et al. 2010; Ripple & Beschta 2012) suggests that landscape context and scale are key considerations for sustainable recovery, where a species-specific approach may be favorable, accommodating mobility, territoriality, and resource requirements of the targeted predator before its reintroduction. Reconstructing habitat features in addition to healthy vegetation communities (windrows) may jumpstart the regeneration of herbivore and predator communities, while autogenic recovery based solely on re-establishing vegetation may not succeed.

Addressing Roadblocks to Management Implementation

Considering the importance of trophic cascades, why are food webs not a major component of restoration project planning? A strong possibility is the time, effort, and expense needed to identify and monitor food webs in ecosystems. Practical solutions for the inclusion of trophic structure in restoration planning can include the following:

- Increase heterogeneity of habitat types across the landscape, which will foster trophic structure. Heterogeneity can be accomplished by plantings of different plant communities in random patches, and the introduction of coarse woody debris in piles or windrows to enhance complexity. This may also require landscape sculpting stream re-configuration to encourage heterogeneity through variation in slope and aspect.
- Increase plant diversity and diversity of plant functional groups on the assumption that plant diversity is positively correlated with the diversity of microbes, fungi, insects, birds, and animals in general, and that biodiversity will increase the stability of the ecosystem.
- Add nesting features such as bird boxes and bee hives to encourage connectivity through pollination and seed dispersal, thus enhancing trophic structure.
- Increase complexity in vegetation structure by planning communities that include combinations of short herbaceous plants, medium-statured shrubs, and tall-statured trees.
- Provide targets for soil development and fungal networks to increase the efficiency of nutrient cycling and environmental stress avoidance, such as drought.
- Add plant litter in terrestrial and aquatic restoration projects, perhaps through the strategic introduction of foundation species, to facilitate decomposition processes and nutrient cycling.
- Manage top-down control by introducing grazing to influence plant diversity and potentially facilitate plant growth.
- Introduce top predators (invertebrate, avian, and mammalian) to trigger trophic cascades.
- Remove non-native top predators, particularly in aquatic systems negatively affected by species invasions.
- Use of genomic tools to characterize the composition and function of predisturbed natural communities, and to monitor recovery during restoration. Although not necessarily as practical a tool as the others, the use of genomics in restoration is a growing field, made more possible by decreasing costs and increased access to better and faster computational power.

Ecologists and restoration practitioners should consider opportunities to coordinate distributed experiments across large geographic scales (Fraser et al. 2013) investigating habitat fragmentation and the complete reorganization of soil, water, and biomass at scales beyond those ordinarily accessible for ecological manipulations or otherwise impractical for single site field experimentation.

Human impacts on the environment, such as continuing natural resource extraction and the disturbance associated with it, require good restoration research and practice. Although food web structures in terrestrial ecosystems are undoubtedly complex, it is possible to evaluate the increased predictive power of whole-ecosystem concepts, over those currently used, making it possible to address fundamental ecological problems in the specific context of human land use.

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