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OPINION ARTICLE

Toward quantitative dryland restoration models

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Developing solutions to restore degraded drylands is one of the largest research challenges of our time. If we are to meet even a fraction of the restoration goals outlined in numerous international programs, we need to find ways to catalyze systematic knowledge development across disciplines that generate cost-effective, repeatable, and scalable solutions for our dryland restoration needs. Ecological models are fundamental to this effort and in this opinion article, we describe the opportunities for building a conceptual understanding of dryland ecosystem function to create realistic systems models to improve seedling establishment in restoration. We do this by first discussing trade-offs among different modeling approaches and then discussing specific recent efforts to develop a systems model for seed enablement for sagebrush steppes systems in the Western United States. We conclude by outlining broader opportunities for integrating systems models to address related dryland restoration challenges and emphasizing the potential complementary aspects that conceptual and systems models may represent in our global efforts to mitigate dryland degradation. As outlined in this special issue, creation of practical solutions will require careful coordination among diverse disciplines. Systems models have been widely used to transcend disciplines to tackle many issues in related fields such as conservation biology and global climate change and should be helpful in making progress toward our dryland restoration goals over the coming decades.

Key words: arid, degradation, invasive plant, rangeland, seed ecology

Implications for Practice

- Addressing our dryland restoration research needs will require sustained collaborative research efforts among research groups and ecological models will play a fundamental role in supporting this collaborative development of knowledge.
- Systems models are one type of quantitative models that have been increasingly used to solve complex problems in conservation biology and other areas in ecology. The field of restoration ecology is well poised to benefit from these approaches.
- To implement this approach, an outcome variable is identified and a hierarchical model of linked ecological processes that influence this variable is constructed. New quantitative data are collected and the differences between observed and expected model outcomes are evaluated and used to refine the model and associated linkages.

Introduction

The critical role that ecosystem restoration will play in mitigating environmental change, increasing food security, and improving political and economic stability over the next century is becoming increasingly clear (Menz et al. 2013; Suding et al. 2015). Developing the science that supports this global restoration need, however, is widely viewed as one of the largest contemporary research challenges. This is particularly true for drylands which support almost a third of the global population (Reynolds et al. 2007; Maestre et al. 2012). Although much of this population directly depends on the health of these systems for their well-being, drylands are some of the systems most susceptible to degradation and environmental change, with estimates suggesting that already 10–20% of global drylands have been degraded, and another 12 million hectares are further degraded each year (Millennium Ecosystem Assessment 2005; Brauch & Spring 2009).

In contrast to more mesic systems, disturbance in drylands regularly produces abrupt changes in vegetation structure, composition, and ecosystem function that are not reversed following disturbance (Young et al. 2001). In many cases, once these systems cross these ecological thresholds they remain in a degraded state (Westoby et al. 1989). In other cases, positive feedback loops initiated by disturbance may be amplified, resulting in even more severe degradation and loss of ecosystem function (Hobbs & Suding 2008). Unfortunately, identifying and developing practical solutions to reverse large-scale dryland degradation has remained out of reach despite decades of intensive research and practice. If we are to reach even a portion of the goals outlined in the numerous dryland restoration programs across the globe over the next decade (e.g. Brauch & Spring 2009; UNCCD 2012), it is essential that in

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a relatively short amount of time we catalyze the development and synthesis of targeted knowledge that allows us to create cost-effective, repeatable, and scalable tools and strategies for dryland restoration.

The scientific knowledge needed to solve dryland restoration issues, even for a given region, clearly exceeds the capacity of any particular individual research program or institution and will therefore require sustained collaborative research efforts among research groups. Ecological models play a fundamental role in supporting collaborative development, synthesis, and application of knowledge and such models will be key in advancing our capacity to restore degraded drylands. The broad goal of this opinion article is to describe the value of using systems models in restoration. To do this, we first briefly compare and contrast conceptual models and quantitative systems models for understanding drivers of dryland restoration outcomes. Second, we examine a detailed case study of how a systems model has been developed and applied, in a relatively short amount of time, to increase the efficacy of native grass seeding efforts in the Western United States. Lastly, we conclude by highlighting key opportunities for refining the use of systems models for restoration of degraded dryland systems across the globe.

Conceptual Versus Systems Frameworks for Dryland Restoration

Conceptual models of plant community assembly have played a critical role in our understanding of how plant communities respond to disturbance and for identifying appropriate restoration interventions. In drylands, state-and-transition models (STMs) were proposed and developed as a way to conceptually describe the often discontinuous and often nonreversible nature of how dryland vegetation responded to disturbance (Westoby et al. 1989; Briske et al. 2006, 2008). These models show potential alternative stable states that could persist at a particular site as well as possible transitions between vegetation states that could be driven by certain combinations of environmental conditions as well as management actions. In these models, transitions are typically considered irreversible without extensive management effort. Although STMs for different dryland systems were originally developed based on observation, a strong theoretical basis for these model predictions has emerged in the literature, particularly in regards to theories and experimental evidence describing thresholds and alternative stable states (Schroder et al. 2005; Suding & Hobbs 2009).

Although there has been clear utility in using STMs and related conceptual models to better understand dryland plant community dynamics, making the necessary rapid advancements in our ability to restore drylands will ultimately depend on our ability to identify, quantify, and manipulate specific ecological processes that drive restoration outcomes. This will require that we expand our conceptual restoration models and develop quantitative models that included the key processes and mechanisms that drive restoration outcomes. The field of restoration ecology is well poised to benefit from these approaches and such a shift in modeling emphasis toward mechanistic systems models is being incorporated into numerous related fields including conservation biology and terrestrial biosphere dynamics (Medvigy & Moorcroft 2012; Norris 2012). Such mechanistic models are fundamental to our understanding of why ecosystem responses to management actions vary, provide important estimates of management uncertainty, and indicate where investment in research and management effort may produce the largest improvements in restoration outcomes.

Broadly, systems models focus on quantifying key processes and mechanisms (e.g. physiological response to stress, competition, colonization) that link different levels of ecological organization (e.g. individual survival, population dynamics, and community structure) and then evaluate how variation in these processes and mechanism drive variation in an outcome of interest. Although a focus on modeling realism over generality comes with trade-offs, including limitations to how the systems particular models can be applied and the relatively data intensive nature of the modeling, the focus on quantitative, mechanistic links between different levels of ecological organization opens up new ways to examine and solve specific restoration challenges. An overall approach to developing a systems model begins with an a priori selection of a subset of key processes and mechanism to include in the model followed by data collection, model testing. Based on these initial results, the key process processes and mechanisms included in the model are refined followed by additional data collection and model retesting. The emphasis here is not to include all mechanisms and processes that influence the outcome of interest but the minimum set of processes and mechanisms that allow outcomes to be predicted with an acceptable level of uncertainty for the question on hand.

All ecological models face trade-offs in terms of model generality, realism and precision (Levins 1966). As any particular model tries to optimize one of these attributes, the models become less capable of capturing the other attributes. Although conceptual models such as STMs may emphasize generality and realism while sacrificing precision, systems models may emphasize realism and precision while sacrificing generality (Evans et al. 2012). A key point here is that these different modeling efforts can be complementary and not mutually exclusive. The value and emphasis of any modeling approach will be determined by the particular restoration question on hand. We use the next section to describe how a systems framework has been developed to address a major dryland restoration challenge in the Western United States.

Systems Model to Improve Native Grass Seedling Recruitment on Drylands

The cold desert sagebrush steppe rangeland in western North America covers over 40 million hectares and provide a suite of critical ecosystem services (West 1983; Meinke et al. 2009). These systems receive much of their precipitation as snow in winter and were historically dominated by perennial grasses, shrubs, and forbs. Over the last century and a half, however, they have become increasingly dominated by invasive annual grasses which have drastically increased the frequency and size of severe fires that destroy the native perennial plant community (D'antonio & Vitousek 1992; Pyke 2003; Taylor et al. 2013). Following these fires, without immediate restoration that includes seeding native perennial grasses, soils are quickly eroded by wind, site hydrology changes, and invasive annual grasses form a persistent monoculture with severely reduced ecological function.

Tens of millions of dollars are spent each year seeding native perennial grasses in these systems following fire in an effort to facilitate site recovery but unfortunately less than 10% of these seeding efforts are successful (Knutson et al. 2009; Sheley et al. 2011). The restoration challenge on hand is substantial as harsh and fluctuating abiotic conditions, competition from invasive annual grasses, environmental change, and altered disturbance regimes all potentially pose large barriers to native perennial grass establishment (Monaco et al. 2003; Boyd & James 2013; Gornish et al. 2015; Schantz et al. 2015). The economics and logistics of native grass restoration serve as additional restoration barriers. Availability of native grass seed is often limited and expensive, and because of limited budgets and time, managers may only be able to treat a small portion of the degraded areas each year (Meinke et al. 2009). Thus, identifying ecological bottlenecks to native grass seedling recruitment and creating management tools and strategies that mitigate these barriers is essential if managers are going to be able to slow and eventually reverse the degradation of these dryland systems with the limited resources available.

Although seedling ecology has long been a central research theme in understanding dryland plant community dynamics and many important insights have been derived from these efforts (e.g. Plummer 1943; Cluff et al. 1983; Leishman & Westoby 1994), the opportunity to incorporate this research around systems models to identify key knowledge gaps and potential unifying management solutions has been largely undeveloped. Over the last several years, however, the foundation of a systems model for managing seed and seedling ecology in sage steppe restoration has been proposed (James et al. 2013). This model is centered on changes in population abundance of sown grass species through time. The model uses a basic plant population life cycle as the highest level of system dynamics, specifying key demographic stages and stage transitions that influence plant population abundance through time (Fig. 1). The second level of this model identifies key ecological processes and mechanisms that drive variation in transition rates between life stages, whereas the third level of the model identifies management tools and strategies that can alter the ecological processes and mechanisms that influence life stage transitions.

Based on these linked hierarchical relationships, the first step for this modeling effort was to identify how variation in key life stage transitions influenced seeded species abundance. Using data from restoration projects across multiple sites and years, sensitivity analysis demonstrated that 30 and 40% of the variation in seeded species abundance 2 years after sowing was associated with variation in the ability of germinated seed to emerge and for juvenile plants to survive their second dry season, respectively (James et al. 2011). Variation in germination rate, seedling establishment, and first year survival contributed substantially less to variation in seeded species abundance. Importantly, patterns of survival across life stage transitions were comparable across the different grass species seeded, providing some indication that basic systems models could be created for functional groups and reduce the number of specific models that would need to be developed.

The second step in this modeling effort was to identify the ecological processes driving variation in the life stage transitions that most influence population abundance, namely emergence and second year survival. Identifying the range of ecological processes that should be included in a systems model can be difficult and in the modeling example described here it is possible to identify a large number of factors that may influence these key life stage transition probabilities. It is important to highlight, however, that with systems model the focus is not on including all possible processes and mechanisms but instead the focus is on identifying a subset of process that may contribute to the majority of the variation in model outcomes.

In the modeling example described here we knew, based on the plant demography work, a substantial portion of population mortality (about 30%) occurred sometime between when seeds germinated but before seedlings emerged. Based on these patterns, we focused investigations on ecological processes that may cause mortality during this period. In sage steppe, this mainly included processes occurring over the cold winter months that followed seed sowing. With this line of research we found that the majority of seeds sown germinate relatively quickly after planting, suggesting seeds are exposed to a number of harsh abiotic and biotic factors over winter that could influence survival including winter drought, freeze thaw cycles, fungal pathogens, and vesicular soil crusts that form as soils dry (James et al. 2011; Boyd & James 2013). Reducing these stresses simultaneously (by increasing snowpack) increased emergence probability by 50% (Gornish et al. 2015). Although these manipulations do not isolate the contribution of individual processes and mechanisms, it is sufficient information to begin to identify new tools and strategies that would mitigate several of these factors.

Based on this systems model described here (Fig. 1), researchers have begun to explore how new types of seed coatings that simultaneously delay germination and reduce negative effects of winter drought and vesicular crusts on germinated seed increase emergence probability (Madsen et al. 2012) while another line of work has examined how variation in key functional traits may reduce the negative effects of these stress on emergence probability (Atwater et al. 2015). Likewise, other research efforts have examined how timing seeding efforts to avoid winter time stress may influence emergence probability (Boyd & James 2013). These different tools and strategies individually are able to increase seedling survival probabilities 3- to 6-fold on sage steppe rangeland. Prior to creating a systems model (Fig. 1), it was difficult to quantify the relative importance of these new management tools and strategies. With at least the basic parts of this model now parameterized it is possible to develop some quantitative assessments of how different management interventions or environmental conditions may influence restoration outcomes.

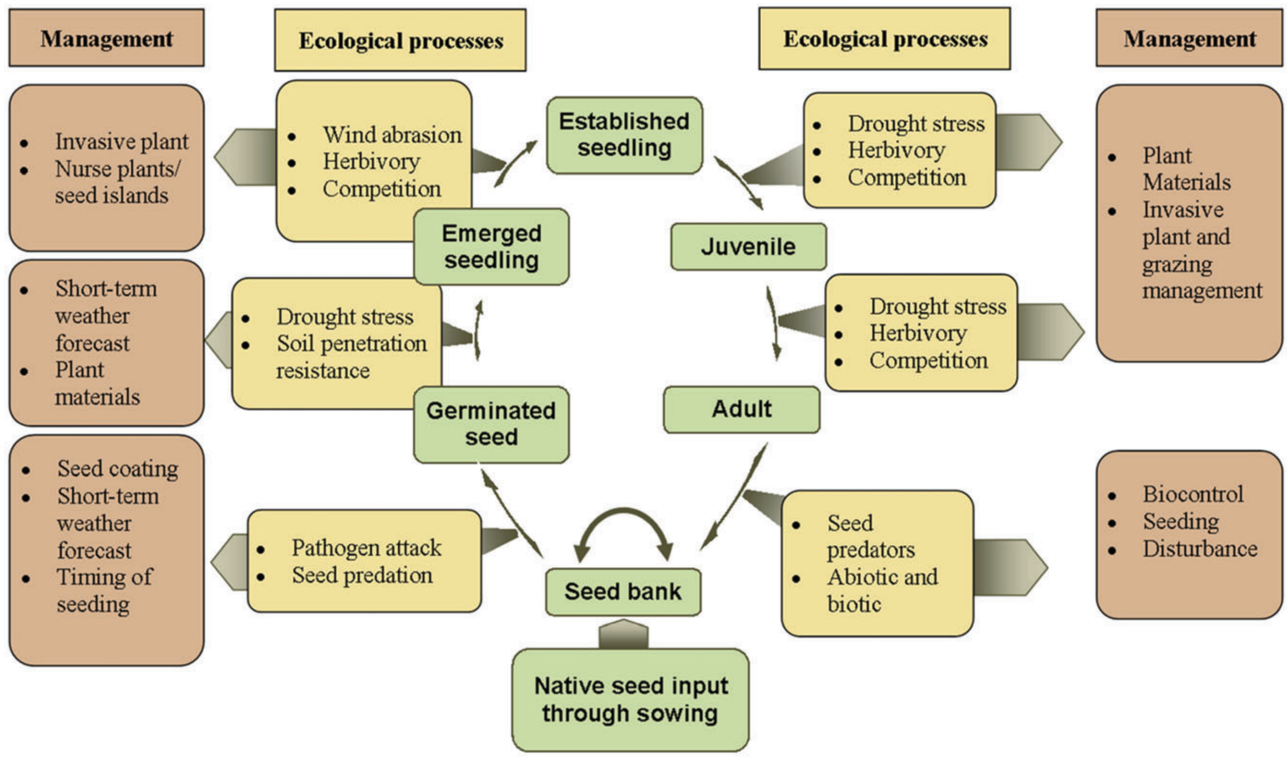

Figure 1. One example of a systems model for seed enablement in dryland restoration. The highest level of ecological organization in this model is represented by a plant population model (inner portion of the model) that specifies key plant life history stages for a wind- or self-pollinating plant. The main model is focused on changes in seeded species abundance through time as the outcome of interest. This outcome is modified by links to other levels of ecological organization including the various ecological processes that influence transition between key life stages and management tools and strategies that could alter these processes. Not all potential processes need to be included in the model but rather a subset of key process that can explain variation in restoration outcomes of concern (modified from James et al. 2013).

Opportunities for Using Systems Models for Global Dryland Restoration Needs

The model described above only represents one example of how a quantitative systems framework could be developed for a particular ecosystem to address a specific aspect of restoration. The key properties and processes included in Figure 1 may not be appropriate for solving other dryland restoration challenges. Accordingly, it is helpful to consider how the general aims of systems framework may be useful to address different restoration challenges across the globe. Systems models could serve several essential functions as researchers, practitioners, and other stakeholder groups strive to meet the mounting dryland restoration needs over the coming decades. First, these models can be progressively modified in terms of the properties quantified, levels of ecological organization included, and the specific processes that are used to link different ecological levels of organization. The systems models described in this article focused on basic systems surrounding population abundance but did not include processes such as density dependence, colonization, or interspecific interactions; all of which may influence population dynamics and rates of vegetation change and could be directly modified through management. As portions of the basic drivers of plant population dynamics become well described, it would be feasible to layer additional model components and potentially develop more realistic forecasts of seeded species abundance. Likewise, in many restoration situations, the emergent properties of concern may extend well beyond species abundance and include effects of vegetation structure and composition on ecosystem functions and services. Systems models would be fully amendable to including quantitative linkages among these different levels of ecological organization to forecast how management inputs that change species abundance may impact flows of different ecosystem functions and services. Ultimately, many of these broader questions (how restoration and management inputs influence species composition, vegetation change, and provision of ecosystem services) are also the focus of many of the current conceptual ecosystem restoration models (Suding & Hobbs 2009). Thus, systems models provide a valuable complement to conceptual models of dryland restoration but differ in that they provide quantitative frameworks to test the hypothesized ecological processes that drive plant community dynamics and ecosystem service provision.

As a second and linked useful role, systems models provide a formal way to organize knowledge, assess the relative importance of different processes or management factors and ultimately help prioritize the most critical information gaps that researchers and managers need to address. Prioritizing research needs and coordinating research efforts among different groups is viewed as one of the largest challenges to our ability to scale up restoration efforts (Menz et al. 2013). Empirical tests of various hypotheses that address theoretical aspects of restoration ecology routinely find significant treatment effects and numerous ecological interactions of interest. What we often cannot do with this suite of information, however, is establish the relative importance of these responses. Quantitative models that lend themselves to sensitivity analysis provide a mechanism to aggregate this information and allow researchers to determine which portions of the system are most important for driving variation in restoration outcomes (Madsen et al. 2012; Boyd & James 2013; Atwater et al. 2015). If these key portions of the system also are poorly understood or associated with large uncertainty, this serves as a useful rationale for prioritizing research and potentially coordinating research efforts across different groups or different disciplines. Numerous disciplines have long relied on systems models to facilitate knowledge sharing and to prioritize research (Evans et al. 2012). It is time that restoration ecologists began to capitalize on these attributes to tackle the complex challenges in restoration ecology.

Lastly, systems models maybe useful for assessing socioeconomic costs and benefits associated with different restoration strategies. Uncertainty associated with practice outcomes plays a major role in determining the expected social and economic cost and benefits of alternative practices (Taylor et al. 2013). Quantitative systems models that include estimates of uncertainty could allow more realistic linkages to be made between ecological and socioeconomic models, allow more accurate assessment of restoration cost and benefits and allow potential trade-offs to be assessed (Failing et al. 2013). The systems model on seed enablement described above provides a simple example of how these quantitative ecological frameworks can help clarify potential socioeconomic trade-offs between different management decisions. Namely, in the example described here, restoration strategies could range from reestablishing specific genetic material to simply reestablishing the fundamental ecosystem functions such as soil stability and water infiltration. Along this spectrum of strategies, potential plant material could include locally collected genotypes of native species, harvested from naturally established field populations, selected and farmed varieties of native species not from the region, or selected varieties of species not native to the region. Different stakeholders may have different restoration goals and thus different preferences for seed source. Portions of the systems model could be developed to estimate the probability that these different restoration strategies using different seed sources could achieve a particular restoration target over a given area for a given cost and, thus, help better describe trade-offs among multiple societal values for different potential management decisions (e.g. stabilizing soils, conserving genetic diversity).

Concluding Remarks

The overall goal of this opinion article is to argue for the possibility of systems model to catalyze the urgent rapid advances we need to solve mounting dryland restoration challenges across the globe. We do not argue that this is the only needed advancement or that these approaches should replace conceptual models of dryland ecosystem function and restoration. Indeed, both systems models and the conceptual STM models discussed here represent only two types of models that exist along a spectrum of potential modeling approaches from conceptual to mechanistic. The most appropriate model is driven by the restoration question on hand. We do argue here, however, that we are quickly running out of time for identifying, developing, and deploying cost-effective, predictable, and scalable solutions for dryland restoration. As outlined in this current special issue, delivering on these outcomes will require careful coordination among soil scientists, engineers, social scientists, industry specialists, plant ecologists and economists. Systems models have been widely used to transcend these disciplines to solve other environmental issues and while not a silver bullet to our global dryland restoration needs they should be fundamental in sustaining measured progress toward these goals over the coming decades.

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