

REVIEW

A systems approach to restoring degraded drylands

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Summary

1. Drylands support over 2 billion people and are major providers of critical ecosystem goods and services across the globe. Drylands, however, are one of the most susceptible biomes to degradation. International programmes widely recognize dryland restoration as key to combating global dryland degradation and ensuring future global sustainability. While the need to restore drylands is widely recognized and large amounts of resources are allocated to these activities, rates of restoration success remain overwhelmingly low.

2. Advances in understanding the ecology of dryland systems have not yielded proportional advances in our ability to restore these systems. To accelerate progress in dryland restoration, we argue for moving the field of restoration ecology beyond conceptual frameworks of ecosystem dynamics and towards quantitative, predictive systems models that capture the probabilistic nature of ecosystem response to management.

3. To do this, we first provide an overview of conceptual dryland restoration frameworks. We then describe how quantitative systems framework can advance and improve conceptual restoration frameworks, resulting in a greater ability to forecast restoration outcomes and evaluate economic efficiency and decision-making. Lastly, using a case study from the western United States, we show how a systems approach can be integrated with and used to advance current conceptual frameworks of dryland restoration.

4. *Synthesis and applications.* Systems models for restoration do not replace conceptual models but complement and extend these modelling approaches by enhancing our ability to solve restoration problems and forecast outcomes under changing conditions. Such forecasting of future outcomes is necessary to monetize restoration benefits and cost and to maximize economic benefit of limited restoration dollars.

Key-words: desert, invasion, restoration, state-and-transition models, thresholds

A global need for improving restoration outcomes in dryland systems

Drylands, which include arid, semi-arid and dry-subhumid ecosystems, cover 40% of the Earth's land surface and support over two billion people, many at subsistence level (Millennium Ecosystem Assessment 2005a). These systems store more than 45% of the global terrestrial carbon (Millennium Ecosystem Assessment 2005b), support 50% of the world's livestock (Allen-Diaz *et al.* 1996) and house over a third of the hotspots of global biodiversity (Myers

et al. 2000). While almost a third of the global population directly depends on drylands for their well-being, low and variable rainfall, as well as other stressors such as low soil nutrient availability, makes drylands one of the most susceptible biomes to land degradation and global climate change (Millennium Ecosystem Assessment 2005a; Reynolds *et al.* 2007). Conservative estimates indicate 10–20% of the global drylands are degraded (Millennium Ecosystem Assessment 2005a) with an additional 12 million hectares of dryland degraded each year (Brauch & Spring 2009). Loss of these critical biomes is estimated to cost the world US \$42 billion a year (Brauch & Spring 2009), reduce dryland potential net primary productivity

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between 4% and 10% (Zika & Erb 2009) and contribute to about 4% of annual global carbon emissions (Millennium Ecosystem Assessment 2005a).

The impacts of dryland degradation on ecosystem sustainability as well as economic and political stability are widely recognized (Daily 1995; Geist & Lambin 2004; Verstraete, Scholes & Smith 2009; UNCCD 2012). National and international programmes identify dryland restoration as key to future sustainability (Bureau of Land Management 2001; Brauch & Spring 2009; McDonald & Williams 2009; Cao *et al.* 2011; UNCCD 2012) with many countries spending over US \$100 million a year on efforts to restore dryland systems (United States Government Accountability Office 2003; Cao *et al.* 2011; Merritt & Dixon 2011). Despite the widely accepted importance of dryland restoration and relatively large amounts of money invested in these activities, restoration success rates in dryland systems are low (Carrick & Kruger 2007; Valladares & Gianoli 2007; Hardegree *et al.* 2011). In the United States, for example, even with application of the most current science, technology and funding models, dryland restoration success rates are often less than 5% (Sheley *et al.* 2011). Thus, while the urgent need for dryland restoration is widely recognized, and globally, much time and money is directed towards these activities, we are strongly limited in our ability to restore these systems.

Despite decades of research, advances in understanding the ecology of dryland biomes have not yielded proportional advances in our ability to restore degraded dryland ecosystems. Here, we propose an approach to accelerate the development of dryland restoration strategies by improving the linkages between the science of restoration ecology and the ability of managers to make practical improvements in restoration outcomes. Specifically, we argue for moving the field of restoration ecology beyond conceptual frameworks of ecosystem dynamics and towards quantitative, mechanistic and predictive systems frameworks that capture the probabilistic nature of how ecosystems respond to management. To do this, we first provide a brief overview of existing conceptual frameworks of dryland restoration. We then detail the value of using systems approaches to accelerate our ability to solve specific restoration problems and make practical improvements in our restoration outcomes. From this, we outline how systems approaches can improve our ability to accurately evaluate the economic efficiency of restoration efforts. Lastly, using a case study from the western United States, we show how a systems approach can be integrated with and used to advance current conceptual frameworks of dryland restoration.

Current conceptual frameworks for dryland ecosystem restoration

Ecological restoration is predominantly focussed on the recovery of functional plant communities as they have a controlling influence on energy flows, hydrology, soil

stability, habitat quality and network dynamics (Young, Petersen & Clary 2005; Kulmatiski, Beard & Stark 2006; Munson, Belnap & Okin 2011; Pooock, Evans & Memmott 2012). As a result, conceptual frameworks for dryland restoration, as well as restoration ecology in general, are largely based on conceptual models of plant community development and response to disturbance. The initial conceptual framework for dryland management and restoration was based on Clementsian succession in which vegetation dynamics were considered linear, continuous and reversible (Briske, Fuhlendorf & Smeins 2003; Vetter 2005; Bagchi *et al.* 2012). Under this framework, changes in abiotic or biotic environmental conditions through restoration were expected to yield proportional, linear changes in plant community structure (Fig. 1a). In many mesic systems, linear-succession models often adequately predicted vegetation dynamics (Young, Chase & Huddleston 2001). However, in dryland systems, fluctuating abiotic and biotic conditions routinely produce discontinuous and nonreversible vegetation changes not captured by linear-succession models (Jackson & Bartolome 2002; Sasaki *et al.* 2009; von Wehrden *et al.* 2012).

The failure of linear-succession models to predict effects of management on dryland plant community dynamics caused ecologists to examine how more contemporary threshold models and community assembly theory could be applied to dryland systems to better predict

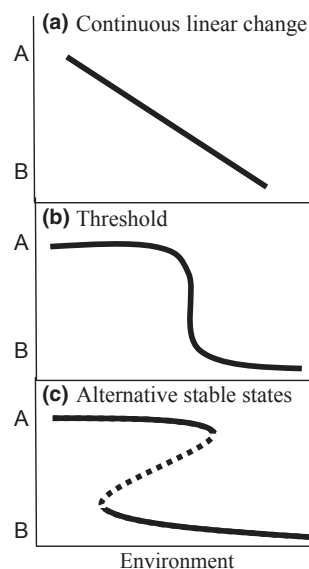


Fig. 1. Ecosystem dynamics models that predict how changes in environmental conditions influence ecosystem state variables A and B (after Schroder, Persson & De Roos 2005; Suding & Hobbs 2009). The Continuous Change model (a) predicts gradual changes in environmental conditions will produce continuous and proportional changes in state variables. The Threshold model (b) predicts little change in state variables over a broad range of environmental conditions until a trigger induces a shift from negative to positive feedbacks and a rapid shift in states. The Alternative Stable States model (c) predicts threshold dynamics as in (b) but also predicts that multiple alternative stable states can persist under similar environmental conditions.

management outcomes (King & Hobbs 2006; Suding & Hobbs 2009; Bagchi *et al.* 2012). These models provide the theoretical basis for understanding how changes in environmental conditions could produce nonlinear, discontinuous changes in plant community structure and how different stable plant community states could form under identical environmental conditions. Threshold models predict little change in ecosystem structure and function over a broad range of environmental conditions until a trigger (e.g. fire, flooding, drought) induces a shift from negative to positive feedbacks, which destabilizes ecosystem dynamics and results in a threshold that produces a rapid shift in ecosystem state variables (e.g. species composition, ecosystem process) (Schroder, Persson & De Roos 2005; Briske, Fuhlendorf & Smeins 2006; Suding & Hobbs 2009) (Fig. 1b,c). In some cases, shifts between states are predicted to be reversible along the same pathway that leads to degradation (Fig. 1b). In other cases, the pathway to restoration is not predicted to be reversible along the same pathway that led to degradation (Fig. 1c). Under this latter scenario, multiple states are predicted to persist under similar environmental conditions. Historical contingencies that influence priority effects are thought to be strong drivers of threshold dynamics (Suding & Hobbs 2009).

The theoretical concepts of alternative stable states, thresholds, nonlinear dynamics and historical contingencies have been useful in describing vegetation dynamics under different management and restoration practices (Hobbs & Suding 2008; Martin & Kirkman 2009; Suding & Hobbs 2009; Zweig & Kitchens 2009; Bagchi *et al.* 2012). A leading aim of dryland restoration ecologists over the last thirty years has been to assimilate these theoretical constructs into conceptual, practical models, to guide improved restoration of dryland systems. A number of applied models have been developed to fill this need (King & Hobbs 2006; Nuttle 2007; Sheley *et al.* 2010). Globally, State-and-Transition models (STMs) have emerged as the leading conceptual framework to describe dryland vegetation dynamics over a range of management and restoration scenarios (Asefa *et al.* 2003; Chartier & Rostagno 2006; Quetier, Thebault & Lavorel 2007; Tietjen & Jeltsch 2007; Sankaran & Anderson 2009; Standish, Cramer & Yates 2009) (Fig. 2). These qualitative models

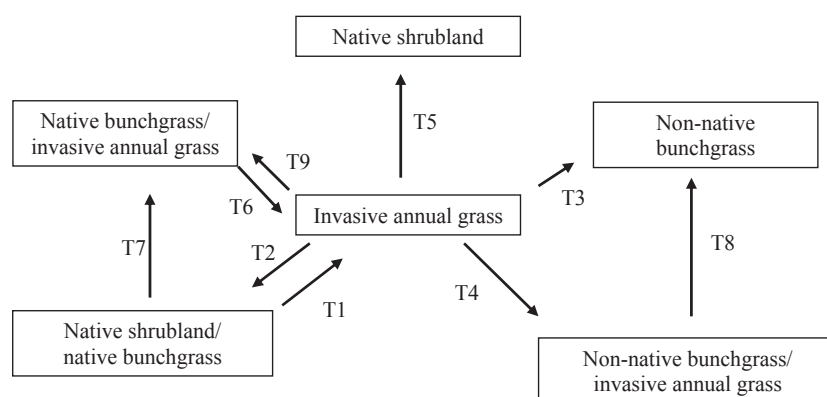
are flowcharts that show potential alternative stable vegetation states supported by a particular combination of soil and climate, as well as possible transitions between states. Transitions represent thresholds between alternative stable states that are generally viewed as irreversible without intensive management inputs. Restoration pathways also are identified in STMs that indicate restoration practices that can reverse transitions between alternative stable states. In most cases, identification of potential alternative states, possible transitions, as well as restoration pathways, are developed based on management experience and expert opinion. The values of these conceptual approaches to dryland restoration are widely recognized and include the ability of models to accommodate theoretical components associated with linear succession, alternative stable states and thresholds. These models also are useful for organizing management information and communicating complex ecosystem dynamics to diverse stakeholders in a simple form (Bashari, Smith & Bosch 2008; Knapp *et al.* 2011).

Despite the utility and application of STMs to global dryland restoration, there are clear and critical weaknesses in these and other related conceptual restoration models that limit our ability to make practical and sustained improvements to dryland restoration outcomes. Namely, these conceptual models have limited predictive capability, do not address management uncertainty and lack the ability to quantitatively link management to multiple ecological processes and mechanisms that ultimately drive ecosystem change. These constraints greatly limit application of conceptual dryland restoration frameworks to scenario analysis and evaluation of economic efficiency which, in turn, constrain the degree to which these models can be used as decision support tools (Bashari, Smith & Bosch 2008).

The need for systems approaches in restoration ecology

The need to move ecology beyond models that are conceptual, mathematically descriptive or phenomenological and towards process-based models that can be used to address specific applied questions is widely recognized (Sutherland & Norris 2002; Levin 2005; Coulson *et al.*

Fig. 2. General state-and-transition model for restoring sagebrush steppe vegetation in the western United States (after Allen-Diaz and Bartolome, 1998). Stable states (boxes) represent distinct stable plant communities. Transitions (T, arrows) indicate thresholds and restoration pathways that move a plant community from one stable state to another. For example, transitions (T) could include restoration actions (e.g. ploughing, herbicide, seeding), management (e.g. grazing) and environmental conditions (e.g. drought, fire).



2006; Suding & Hobbs 2009; Evans 2012). This need for process-based models has become progressively more urgent in the light of rapid environmental change (Evans 2012). Systems approaches have long been recognized as a critical means to fill this need (Watt 1968). Adoption of these approaches, however, has been limited (Norris 2012). Recently, there have been renewed arguments for and examples of using systems approaches to address specific, complex problems in ecology (Purves & Pacala 2008; Morin & Thuiller 2009; Butler *et al.* 2010; Medvigy & Moorcroft 2012; Norris 2012). A logical next step is to examine the utility of adopting systems approaches for ecosystem restoration.

Selecting a modelling approach to solve an ecological problem involves considering trade-offs between model generality, model realism and model precision (Levins 1966; Odenbaugh 2003; Evans 2012). A systems approach to solving ecological problems differs philosophically, structurally and procedurally from other quantitative modelling approaches. Systems approaches, by definition, explicitly consider specific characteristics of a particular system and are thus models focussed on realism and how a specific system functions (Evans 2012; Evans, Norris & Benton 2012). In general, a model based on a systems approach would include mechanisms driving ecological processes within model components and also would identify ecological processes that establish hierarchical links among system components (Evans 2012; Evans, Norris & Benton 2012; Norris 2012). With this approach, attributes of the highest system component in the hierarchy are quantified as emergent properties of model components lower in the hierarchy (Evans 2012; Evans, Norris & Benton 2012). There are several strengths of a systems approach over other modelling approaches. As one example, in contrast to phenomenological models, systems models do not need to assume that model relationships remain similar across all conditions because they specify the underlying mechanisms and processes that drive model behaviour (Evans 2012). Thus, systems models are useful for projecting system behaviour under novel conditions such as environmental change (Evans 2012). As a second example, in contrast to models describing general mathematical relationships, systems models make realistic predictions that can be applied to a specific ecological problem (Evans 2012). Specific predictions allow model error, uncertainty and sensitivity to be assessed while also identifying key knowledge gaps. Systems models have demonstrated clear utility in solving major ecological problems including biodiversity conservation, forecasting ecosystem response to climate change, as well as for climate change modelling (Butler *et al.* 2010; Evans 2012; Medvigy & Moorcroft 2012). The field of restoration ecology is well poised to adopt these approaches, as has been done in these other fields. One of the largest benefits of using quantitative systems models to forecast restoration outcomes is in evaluating economic efficiency of alternative restoration actions.

Systems approaches and the economics of restoration

Economics plays a central role in restoration ecology (Naidoo *et al.* 2006; Robbins & Daniels 2012). By quantifying the benefits and costs of restoration activities in a common unit (dollars), economic analysis allows the economic efficiency of specific restoration projects to be evaluated and compared against alternative projects, including the option of doing nothing. Economic analysis also is central in determining where scarce land management resources should be directed across the landscape to maximize expected economic benefit from restoration given relevant biophysical and financial constraints (Newburn *et al.* 2005; Naidoo *et al.* 2006). Much of the literature outlining linkages between restoration and economics, however, has focussed on how the costs and benefits of restoration should be quantified and how restoration of critical ecosystem services should be funded (Holl & Howarth 2000; Aronson *et al.* 2010; Robbins & Daniels 2012). Largely missing from this discussion is how our ability to develop accurate cost-benefit analyses entirely depends on our ability to predict restoration outcomes. In this section, we outline why quantitative models that allow prediction of restoration outcomes are necessary for accurate cost-benefit analysis of specific restoration strategies, including cases where the ultimate outcome of restoration is uncertain. As support for this argument, we use a case study to demonstrate how restoration success probability influences the expected net economic benefits of restoration.

Historically, economic analyses of ecological restoration in dryland systems have used a number of *ad hoc* approaches (expert opinion, consensus papers, etc.) to parameterize conceptual ecological models to compare how ecosystems would change with and without restoration treatments (e.g. Epanchin-Niell, Englin & Nalle 2009; Taylor *et al.* 2011). These *ad hoc* methods have a number of potential weaknesses including bias, lack of scientific support and the fact that different *ad hoc* methods may yield different parameter values. Quantitative ecological models, on the other hand, avoid these limitations and allow for more realistic predictions of ecological trajectories of treatment sites under alternative restoration treatment strategies, including the alternative of not pursuing any restoration treatment. The economic benefits of restoration are measured as the difference in the flows of monetized ecosystem goods and services under the two alternative ecological trajectories for the site. Success rates of restoration treatments play a large role in determining their expected economic benefits. Quantitative restoration models allow us to identify how variation or manipulations of certain processes or environmental conditions influences the likelihood of a successful restoration outcome (McBride *et al.* 2010). This allows managers and researchers to conduct sensitivity analysis to determine which portion of the system can be manipulated to yield

the largest increase in the probability of a successful outcome, and, hence, the expected economic benefits from restoration. The ability to account for uncertainty is particularly important for the economics of ecological restoration, where avoiding instances of the least desired outcome may be more important than the average outcome when evaluating the desirability of a specific restoration project. Below we show how quantitative ecological models that improve our ability to predict restoration outcomes or increase the probability of restoration success can greatly advance our ability to assess economic efficiency of management alternatives and allocate limited restoration resources.

THE ECONOMICS OF RESTORING DRYLAND ECOSYSTEMS IN THE WESTERN UNITED STATES

This section presents an example of the economics of ecological restoration for two dryland ecosystems in the western United States: the Wyoming Sagebrush Steppe (WSS) and Mountain Big Sagebrush (MBS) ecosystems. In both ecosystems, ecological restoration is focussed on returning the system from a degraded, invasive grass dominated state, to a healthy ecological state dominated by native plants. This example considers the benefits of ecological restoration in terms of a single emergent property of the ecosystem: wildfire activity, with degraded invasive plant-dominated communities having more frequent and severe wildfire than healthy native plant-dominated communities.

In order to evaluate the economic returns from restoration, an economic simulation model was used that incorporates the probability of the plant community transitioning between healthy and degraded states under different restoration scenarios. Each run of the simulation model considers ecosystem change with and without restoration treatment over 200 years with different randomly generated realizations of random parameters (wildfire occurrences, treatment success given that treatment is undertaken, and per hectare wildfire suppression costs) in each year. The economic benefit of a restoration treatment is calculated as the present value of the reduction in wildfire suppression costs resulting from treatment over the 200-year period less the present value of treatment costs. A description of the data used to parameterize these models is given in the study by Taylor *et al.* (2011).

We determined the break-even treatment cost for a range of treatment success rates for the WSS and MBS dryland systems (Fig. 3). The shaded region below the curve contains all of the treatment cost/success rate combinations for which the economic benefits of restoration are greater than the costs. The default current restoration cost is US \$408 hectare⁻¹ and is based on typical dryland restoration treatment costs for these systems, including a combination of prescribed fire, herbicide and seeding (http://www.ut.nrcs.usda.gov/technical/technology/economics/2011_cost_data_practices.html). At this current per hectare

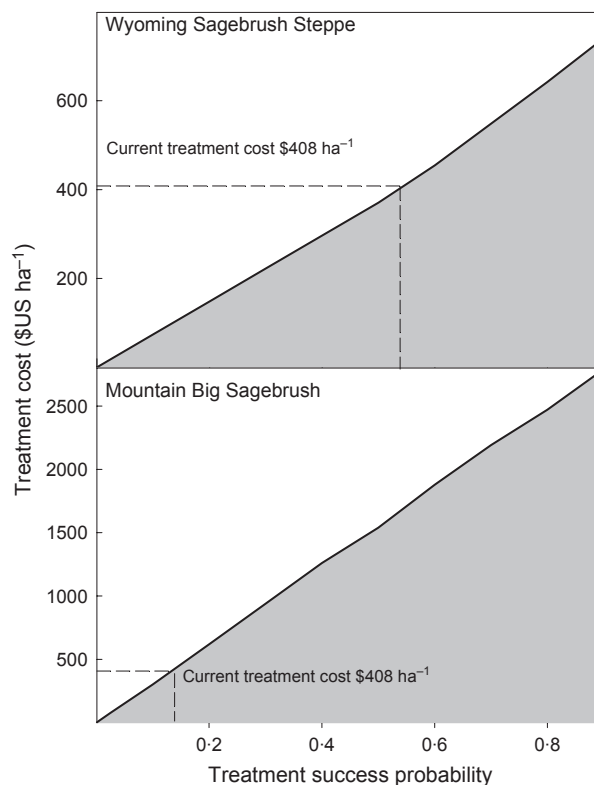


Fig. 3. The break-even treatment cost for a range of treatment success rates for the Wyoming Sagebrush Steppe (WSS) and Mountain Big Sagebrush (WBS) dryland systems. The shaded region below the curve contains all of the treatment cost/success rate combinations for which the economic benefits of restoration are greater than the costs. The default current restoration cost is US \$408 hectare⁻¹. At this current per hectare cost, treatment alternatives in the WSS are economically efficient if success probability exceeds 0.52, while treatments in the MBS are economically efficient if success probability exceeds 0.15. Modified from Taylor *et al.* (2011).

restoration cost, restoration treatment in the WSS ecosystem is economically efficient only if treatment success rate exceeds 0.52. In the MBS ecosystem, treatment is economically efficient with only a moderate success rate of 0.15 or higher. The break-even restoration treatment cost for a given treatment success rate is lower for the MBS system than for the WSS system because the expected benefits from restoration are higher in MBS systems. The expected benefits from restoration are higher in MBS systems primarily because the fire suppression costs in degraded MBS are higher than in degraded WSS (Fig. 3). In particular, the expected present value of wildfire suppression costs over the 200-year period for remaining in the degraded invasive plant-dominated state is \$3577 hectare⁻¹ in MBS compared with \$985 hectare⁻¹ in WSS.

These results demonstrate the need to develop economic models that incorporate forecasts from quantitative systems models. These linkages are critical in evaluating the anticipated economic benefits from restoration and accounting for uncertainty in how ecosystems respond to restoration treatments and other management actions.

Linked economic and ecological models are critical in considering the economic return of realistic changes in management strategies that influence both treatment costs and success rates. In addition, economic models linked to quantitative ecological models are amenable to sensitivity analysis where the benefits and cost of alternative management strategies for ecological restoration could be analysed and compared. While the utility of developing quantitative models to forecast restoration outcomes and evaluate economic efficacy of alternative management actions may be easy to recognize, it may be less clear how to integrate systems models with current conceptual dryland restoration frameworks. This notion is explored below using an example of dryland restoration in the western United States as a case study.

Case study integrating systems models with conceptual dryland restoration frameworks

Sagebrush steppe rangelands occupy over 36 million hectares in western North America and provide a suite of goods and service essential for maintaining rural economies and sustainable agricultural practices key to global food production. Over 25% of these critical drylands, are degraded and an additional 100 000 hectares are estimated to be lost each year due to an expanding cycle of catastrophic fire and invasive plant spread in which large, frequent fires favour invasive plant spread and the spread of invasive plants favours larger and more frequent fires (D'Antonio & Vitousek 1992). Stakeholder groups in this region recognize that active restoration is critical to stem the loss of these drylands and avoid collapse of a keystone agricultural industry and the associated ecosystem services these drylands provide (Bureau of Land Management 2001). Restoration in these systems typically centres on native plant seeding following catastrophic wildfire as a means to stabilize soil, recover the forage base and break invasive plant driven changes in fire regimes. Over US \$100 million is spent annually by government agencies and conservation groups to restore these degraded drylands yet less than 10% of these restoration efforts are successful (Sheley *et al.* 2011).

The seriousness of these restoration failures is widely recognized, and dryland researchers and managers in the western United States have spent decades trying to improve success rates of native plant restoration. This effort has yielded a large number of site-specific empirical studies identifying mechanisms that influence individual plant processes such as establishment, growth and survival (Hardegree *et al.* 2011). At the same time, researchers and managers have developed over 2000 State-and-Transition models (STMs) that provide the conceptual basis for how dryland restoration and management should be implemented (e.g. Fig. 2) (Knapp *et al.* 2011). While these efforts have contributed to improved understanding of dryland restoration, the inability to quantitatively integrate individual studies on seedling establishment and link

conceptual STMs to these mechanistic studies has limited the ability of researchers and practitioners to make sustained, broad-scale advances in improving native plant restoration outcomes. A quantitative systems framework that can organize and integrate current understanding across individual studies, identify key knowledge gaps and direct future research and management efforts may be one way to foster large advances in dryland restoration.

We developed and applied a quantitative systems model as a mechanism to facilitate, integrate and advance research on native plant restoration in sage steppe systems (Fig. 4). This model structure closely follows approaches used in invasive plant management and conservation biology, and here, we show how this basic structure can be used as a systems approach to address restoration issues. Population growth rate and abundance of seeded species is identified as the emergent property of concern in this model. This emergent property was chosen because STMs and assessments of dryland restoration success centre on the abundance and persistence of dominant native plant species. The second level of this model identifies ecological processes and conditions that influence the transition of native plant species across key life stages. The third level of this model identifies management tools and strategies that can alter ecological processes and conditions that influence life stage transitions. We used the existing literature to identify the most likely ecological processes and conditions that influence life stage transitions as well as the available management tools and strategies that may alter these ecological processes and conditions. This systems model can complement the current STM approach used by managers and advance this conceptual framework by providing a quantitative and mechanistic basis to predict how management may influence restoration and changes in plant community states. While this model is relatively simple, it contains the key attributes of a systems approach. Namely, the multiple ecological processes across levels of organization are quantitatively linked allowing probabilistic and predictive estimates of emergent properties to be made under observed and novel conditions and sensitivity analysis to be performed.

To develop parameter estimates for the population model, we monitored transition probabilities for the key life stages shown in Fig. 4 for three dominant restoration species at one site for 3 years as well as for a mixture of restoration species at four sites in 1 year (James, Svejcar & Rinella 2011). Sensitivity analysis demonstrated that the transition from a germinated seed to an emerged seedling was the most important transition determining the abundance of native species as well as variation in density across species, sites and years with conditional survival probabilities during this critical life stage transitions varying from less than 0.05 to more than 0.7 depending on species, year and site. With the systems model, we then used the existing literature and experimental manipulations to identify suites of processes and conditions that may influence this critical life stage transition. Winter time

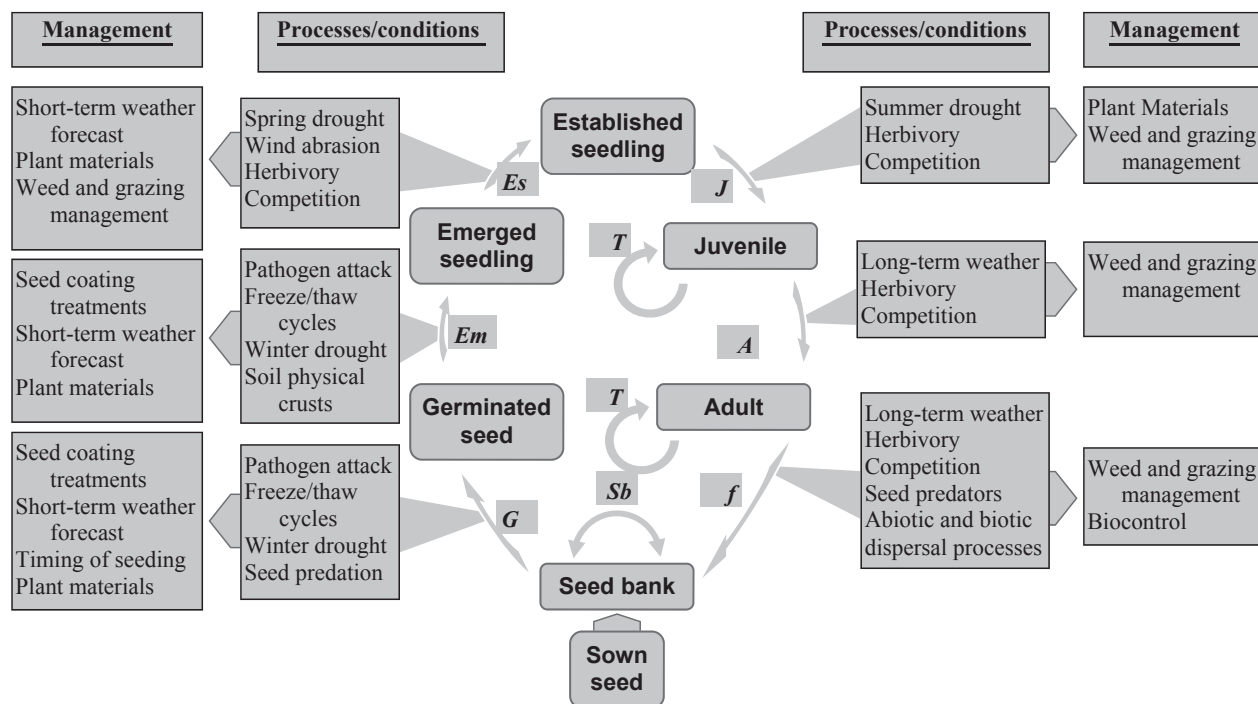


Fig. 4. An example of a restoration model developed based on a systems approach. The model contains three hierarchically linked components. The model component highest on the hierarchy (population growth model, centre of figure) directly yields plant population growth rate or abundance as possible emergent properties. This model describes major demographic stages (e.g. seed bank, germinated seed) and transition probabilities between stages (e.g. G , Em , Es). The next level of the hierarchy is the key ecological processes and conditions that influence demographic transition probabilities. The third level of the hierarchy is management tools and strategies that can alter and mitigate specific ecological processes and conditions that influence transition probabilities between demographic stages. The overall goal is to quantitatively link key ecological processes or conditions to transition probabilities to identify major drivers of population growth rate. This assessment is then used to guide selection and development of management strategies that mitigate or alter key processes and conditions.

soil temperature and moisture conditions, fungal pathogen attack on germinated seed, and formation of soil surface crusts have been identified in the literature as likely processes and conditions that would have a major influence on these transition probabilities (Crist & Friese 1993; Belnap 2003; Hardegree, Flerchinger & Van Vactor 2003). In the case of soil surface crusts and soil microclimatic conditions, process-level models are available that predict the magnitude of the effect of these factors on transition probabilities (Frelich, Jensen & Gifford 1973; Belnap 2003; Hardegree, Flerchinger & Van Vactor 2003). The linkages between the plant population models and the soil processes models have allowed researchers and managers to identify critical knowledge gaps and develop new management tools. This includes the use of microclimate field data to develop predictions of seedbed favourability for emergence and determine how this varies among native species (Hardegree *et al.* 2011), development of seed coating technology that reduce fungal attack and increase the ability of native species to emerge in soils with a pronounced vesicular layer (Madsen *et al.* 2012), as well as identification and selection of functional traits that maximize emergence probability (Rowe & Leger 2011). Collectively, this systems approach complements and advances the conceptual STMs commonly used to guide restoration by providing a quantitative framework

for predicting effects of management and ecological conditions on restoration outcomes and vegetation state changes.

Concluding remarks

Ecosystem restoration involves recreating complex, linked, biotic and abiotic networks. Achieving this goal in dryland ecosystems has been difficult, and even restoring system components (e.g. establishing plants) has been elusive. Although still an emerging science, restoration ecology has focussed heavily on the use of conceptual theories and models to reverse ecosystem degradation. Conceptual models have been useful for formulating general guidelines about how dryland ecosystems may respond to management. However, the chronic and widespread dryland restoration failures observed worldwide demand that we move from conceptual models that allow formulation of general principles and towards quantitative systems models that allow practitioners to identify and manipulate specific ecological processes driving restoration outcomes.

As we have shown in our case study, quantitative systems models can be developed to greatly accelerate understanding and the development of practical management solutions for specific restoration challenges. A reasonable question, however, is how we transfer this general concept

and case study to different restoration scenarios. Similar to our approach, most of the successful applications of systems models in the literature use well-developed conceptual models as a basis. These conceptual models are useful for indicating direction and magnitude of potential model components and reasonable boundaries for potential processes and mechanism that might be included in the model. The second common thread among successful examples is the ability to identify a central emergent systems property (in our case study, here it was native plant density) and quantify the major direct and indirect processes and mechanisms that drive most of the variation in this property. Systems models are not focussed on exact predictions so not every process and mechanism needs to be included. Instead, these models aim to include a minimum subset of model components that allow predictions to be generated as a distribution of likely values. How broad or narrow the distribution lies is dependent on management objectives and tolerance for uncertainty in management outcomes.

There are trade-offs in using systems models, however, and not every restoration challenge lends itself to a systems approach. Systems models are developed for a specific system, and individual models have limited ability to generate general principles (Evans 2012). If system boundaries and system heterogeneity are poorly defined, these quantitative models may poorly predict system dynamics. In addition, if general management or restoration principles are poorly developed, it may be difficult to reliably construct a quantitative model that accurately predicts system dynamics. Systems models also are data intensive, taking time and resources to develop (Norris 2012). This large resource demand requires coordination and data sharing among researchers and sustained funding of research to develop the appropriate systems model. Not every restoration issue has this type of sustained support. Lastly, as occurs with all modelling efforts, systems models require researchers to decide which processes, mechanisms and system components to include and these decisions ultimately influence model outcomes (Evans 2012). Moving forward, restoration ecologist and practitioners will need to consider how these potential limitations associated with systems models relate to the specific restoration challenge on hand.

Healthy ecosystems are essential for sustaining life but are being degraded at alarming rates worldwide (Travis 2003; Hindmarch, Harris & Morris 2006). Our ability to restore degraded ecosystems is central to regaining the essential goods and services provided by these ecosystems. In spite of substantial importance and effort, restoration of degraded dryland ecosystems remains mostly unattainable (Carrick & Kruger 2007; Hardegee *et al.* 2011; Sheley *et al.* 2011). Conceptual models have provided a basis for understanding and improving dryland restoration success. To be useful to managers, these models will need to be advanced to allow for identification and development of site-specific solutions to restoring ecosystem structure and function. Great opportunities for improving

our ability to restore dryland ecosystems exist by combining conceptual models with systems modelling approaches. Systems models can help overcome restoration limitations by allowing site-specific outcomes to be forecasted and enhancing our ability to identify and solve site-specific problems.

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