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TOWARD PREDICTION IN THE RESTORATION OF BIODIVERSITY

Where and how to restore in a changing world: a demographic-based assessment of resilience

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Summary

1. Managers are increasingly looking to apply concepts of resilience to better anticipate and understand conservation and restoration in a changing environment.

2. In this study, we explore how information on demography (recruitment, growth and survival) and competitive effects in different environments and with different starting species abundances can be used to better understand resilience. We use observational and experimental data to better understand dynamics between native *Stipa pulchra* and exotic *Avena barbata* and *fatua*, grasses characteristic of native and invaded grasslands in California, at three different levels of nitrogen (N) representative of a range of pollution via atmospheric deposition. A modelling framework that incorporates this information on demography and competition allows us to forecast dynamics over time.

3. Our results showed that resilience of native grasslands depends on N inputs, where natural recovery should be possible at low N levels whereas native persistence would be difficult at high N levels. Hysteresis was evident at moderate N levels, where the starting conditions mattered.

4. *Synthesis and applications.* The resilience of both invaded and native grasslands is influenced by nitrogen inputs. Our modelling approach gives direction about how best to allocate limited management resources as baselines shift: where natural recovery is possible, where best to allocate active restoration efforts, and where native remnants may be most vulnerable.

Key-words: California grasslands, competition, demography, discrete population model ecological resilience, feedbacks, hysteresis, management prioritization, nitrogen enrichment

Introduction

Natural systems are experiencing unprecedented rates of change that can compromise biodiversity and ecosystem functioning (Newbold *et al.* 2015). Faced with this uncertain future, resource managers are increasingly setting goals related to ecological resilience – the capacity of an ecosystem to reorganize and recover processes – to better anticipate and manage for future change (Holling 1973; Resilience Alliance 2010; Mitchell *et al.* 2014). While we have made significant advances in our conceptual understanding of ecological resilience (Suding & Hobbs 2009; Biggs *et al.* 2012), it has been challenging to apply this

deceptively simple concept (Hallett *et al.* 2013; Standish *et al.* 2014).

One of the key challenges in managing for resilience is the consideration of feedback processes (associated with biotic interactions, disturbance regimes, or propagule pressure) that can promote different community states under similar environmental conditions (Lewontin 1969; Schroder, Persson & De Roos 2005). For example in the cold deserts of the Great Basin, fire and grazing disturbances create feedbacks that determine whether an area persists as a native sagebrush community, a mixed sagebrush-annual invader community or an annual invader community (Chambers *et al.* 2014). These feedbacks can also create hysteresis, where the actions needed for recovery are different than reversing the actions that led to the degradation (Suding, Gross & Houseman 2004). Identifying feedbacks and the presence of hysteresis is, however, notoriously difficult (Schroder, Persson & De

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Roos 2005). The fact that the presence and nature of these feedbacks can change as the environmental baseline changes further compounds the challenge (Scheffer *et al.* 2001; Suding & Hobbs 2009; Standish *et al.* 2014).

One avenue forward is to leverage experimental and observational studies to forecast dynamics that can be used to identify the various components that create, maintain, or disrupt resilience (Hansen *et al.* 2013; Dakos *et al.* 2015). Here, we explore how demographic models that take into account species interactions in different environments and with different initial abundances can be used to better understand resilience. There is a rich body of literature using demographic modelling to evaluate when systems – generally characterized by the dominant species or a key functional group – may resist or be susceptible to invasion by another species or functional group (Levine & HilleRisLambers 2009; Mordecai *et al.* 2015). This approach can similarly be applied to infer whether systems are stable, have low resilience, or given the right starting conditions, can convert to an alternate state. By understanding dynamics through time, this approach can examine how resilience may change as the environment changes (e.g. Borer *et al.* 2007; Pathikonda *et al.* 2009), allowing managers to better understand trajectories of systems over timescales longer than the short windows usually allocated for decision making (Dickens & Suding 2014). We employ a broad definition of resilience (after Standish *et al.* 2014), with a focus on compositional trajectories and basins of attraction rather than effects of a particular type perturbation.

California grasslands are emblematic of landscapes where managing for resilience is paramount. These grasslands provide important ecosystem services as rangelands (Andersen *et al.* 2002) and are home to a diverse group of endemic species (Myers *et al.* 2000). They are also some of the most invaded grasslands in the world: 9·2 million ha of Californian grasslands have been invaded by annual Mediterranean grasses introduced in the 19th century (Heady 1977). Once invaded, recovery has often been slow or non-existent (Stromberg & Griffin 1996). However, remnant patches of native bunchgrasses appear to resist invasion (Hamilton 1997). Experimental work as well as recent modelling suggest feedbacks may allow both types of vegetation to persist (Seabloom *et al.* 2003; Corbin & D'Antonio 2004; Mordecai *et al.* 2015).

Atmospheric nitrogen (N) deposition has become a widespread stressor to natural ecosystems worldwide (Fenn *et al.* 2010). In California, increased N deposition may increase the susceptibility of native grasslands to invasion, particularly in areas where feedbacks established by the native species are reset by disturbance (Allen *et al.* 1998; Hoopes & Hall 2002). Deposition patterns can be both regional and local in nature, affected by the movement of regional climate systems as well as proximity of major sources of emission, such as roads and industry (Weiss 1999; Fenn *et al.* 2010). Increasingly, management priorities include understanding how increasing N inputs may affect the vulnerability of remnant native stands to invasion as well as how these inputs may influence the success of native grassland restoration.

Here, we illustrate how demographic models can be used to help anticipate and better understand how increasing N deposition will affect the conservation and restoration of native grasslands in California. Across differing N inputs, we investigate two management challenges: (i) how to enhance the invasion resistance of remaining native grasslands (in areas with native starting conditions) and (ii) how to optimize the success of restoring invaded grasslands (in areas with exotic starting conditions). We used empirical data to populate models for exotic and native grasses, whose coexistence or dominance we simulated under different N scenarios. We conclude by translating model results to potential management strategies that could be integrated into an adaptive management plan.

Materials and methods

STUDY SYSTEM

We focused on grasses that characterize native and invaded areas in California grasslands: *Stipa pulchra*, a perennial bunchgrass and the annual grasses of the genera *Avena* (*Avena barbata* and *Avena fatua*) (Heady 1956; Hull & Muller 1977; Larios, Aicher & Suding 2013; hereafter *Stipa* and *Avena*, nomenclature follows Baldwin *et al.* 2012). We selected these two species based on observations of co-occurrence in previous studies (Hull & Muller 1977; Larios, Aicher & Suding 2013). We further focused on *Avena*, which has been historically described as a dominant non-native in invaded areas (Heady 1956), as it readily outcompetes and gains dominance in the presence of the other non-native annuals (Gulmon 1979). While these species have been the focus of ecological study and restoration for decades, efforts to understand their dynamics via demographic models are recent and developing (e.g. Borer *et al.* 2007; Corbin, Dyer & Seabloom 2007; Mordecai *et al.* 2015).

California grasslands are characterized by a Mediterranean climate with the growing season restricted to the period of precipitation, which falls between September and May. Most seeds germinate after large rain events in the fall, and both annual and perennial species produce the majority of their seeds at peak biomass in late April and early May. We used data predominately from sites in Southern California (South Coast Research and Extension Center and the Irvine Ranch National Landmark, both in Irvine, CA, USA), where the average growing season rainfall from 1991 to 2010 was 338·5 mm and mean growing season temperature was 21 °C (California Irrigation Management Information Services, http://wwwcimis.water.ca.gov). We supplemented data from these sites with data from Sierra Foothills Research and Extension Center (Browns Valley, CA) and Vasco Caves Regional Park (Livermore, CA), which receive somewhat different rainfall (657.6 and 294.3 mm for 2001–2013 respectively).

POPULATION GROWTH MODELS

We used a discrete-time population growth model to describe the number of individuals (for the annual *Avena*) and the number of seedlings and adults (for the perennial *Stipa*) at the peak growing season in spring. We modelled this as a closed system with no dispersal in or out of the system at a small spatial scale (1 m²);

however, model dynamics are applicable to larger spatial scales (>20 m^2), where *Avena* and *Stipa* have been observed to co-occur on a landscape (Larios, Aicher & Suding 2013). To quantify competition we used a Beverton–Holt function commonly used in similar analyses (e.g. Levine & HilleRisLambers 2009; Mordecai *et al.* 2015), which adjusts growth rate by competitive interactions with other species. Below we outline, how we applied this approach to the life history of these species.

As annual grasses, *Avena* recruits from seed and reproduces in a single growing season. It experiences competition both upon recruitment (i.e. the number of established adults at the end of the growing season) and seed production; however the source of competition varies at these stages. For example, *Avena* germinants are subject to strong self-thinning during the growing season (Young, Evans & Kay 1981). Consequently, *Avena* recruitment patterns are primarily a function of intraspecific competition (eqn 1). Therefore, we modelled *Avena* recruitment as follows:

$$N_{A,t+1} = \frac{g_a r_a}{1 + \alpha_{aa} g_a N_{a,t+1}} N_{a,t+1}, \qquad \text{eqn 1}$$

where $N_{A,t+1}$ represents the number of *Avena* individuals at peak growing season in year $t + 1$. The number of *Avena* individuals ($N_{A,t+1}$) depends on the number of input seeds ($N_{a,t+1}$), the fraction of those seeds that germinate (g_a) and the fraction that subsequently recruit (r_a), which is modified by intraspecific competition with other germinants within year $t + 1$ (α_{aa}). We assumed that all recruited *Avena* individuals reproduce, but their seed production is influenced by both intra- and interspecific competition. Avena seed production is strongly correlated to its size at peak growing season (L. Larios & K.N. Suding unpublished data); therefore, concurrent biomass accumulation of neighbours can reduce individual *Avena* growth and thus fecundity. We omitted the presence of a seedbank as seed mortality (Borchert & Jain 1978) and high germination rates (Young, Evans & Kay 1981) result in about one percent of seeds going into the seedbank (Young & Evans 1989). Therefore, we modelled *Avena* seeds at the beginning of the following growing season ($N_{a,\,t+1}$) as

$$N_{a,t+1} = \frac{N_{A,t}\lambda_A}{1 + \alpha_{AA}N_{A,t} + \alpha_{Ap}N_{p,t} + \alpha_{AP}N_{P,t}}, \qquad \text{eqn 2}$$

where $N_{A,t}$ represents the number of *Avena* individuals at peak growing season in year t and $N_{a,t+1}$ represents the number of *Avena* seeds at the beginning of the following growing season, while $N_{p,t}$ represents the number of *Stipa* seedlings and $N_{P,t}$ represents the number of *Stipa* adults at peak growing season in year t. The number of *Avena* seeds in year $t + 1$ ($N_{a,t+1}$) depends on the number of *Avena* individuals at peak growing season in year t ($N_{A,t}$), the per capita seed production of those individuals in the absence of competition (λ_A) and the reduction in seed production due to intra- and interspecific competition (α_{AA} and α_{Ap} α_{AP} respectively).

As a perennial species, *Stipa* initially recruits from seed to a seedling stage. This seed originates from the previous year as there is minimal seedbank carryover (Major & Pyott 1966; Bartolome 1979). We assumed seedlings are not reproductive in their first year, but those seedlings that survive a full year become reproductive adults in subsequent years. Because of this reproductive distinction we modelled *Stipa* seedlings (eqn 3) and adults (eqn 4) separately. We first modelled *Stipa* seedlings as follows:

$$N_{p,t+1} = \frac{N_{P,t}p_P\lambda_P}{1 + \alpha_{PP}N_{P,t}}r_p, \qquad \text{eqn 3}$$

where the number of *Stipa* seedlings in year $t + 1$ ($N_{p,t+1}$) depends on the number of *Stipa* adults in year t ($N_{P,t}$), the probability that an adult will reproduce (p_P), the per capita seed production of reproductive adults in the absence of competition (λ_P) and the reduction in seeds produced due to intraspecific competition among adults (α_{PP}), as we expected that *Stipa* adults would compete primarily with each other based on previous empirical studies (Corbin & D'Antonio 2004). We then multiplied by the fraction of seeds that germinate and recruit (r_p). Within their first year, seedlings grow and compete both with themselves and other annual grasses like *Avena* (Dyer & Rice 1997). The strength of these competitive interactions affects seedling growth and ultimately the likelihood that a seedling will survive the summer drought to transition to an adult. We therefore modelled *Stipa* adults as follows:

$$N_{P,t+1} = \frac{N_{p,t}s_p}{1 + \alpha_{pp}N_{p,t} + \alpha_{pA}N_{A,t}} + s_P N_{P,t}, \qquad \text{eqn 4}$$

where the number of *Stipa* adults time $t+1$ ($N_{P,t+1}$) depends on the fraction of *Stipa* seedlings in year t ($N_{p,t}$) that survive to become adults (s_p), which is reduced by intra- and interspecific competition (α_{pp} and α_{pA} respectively), and on the number ($N_{P,t}$) and survival of adults from the previous year (s_P). We additionally assumed that parameter values on average capture the dynamics of *Stipa* adult survival and seed production. Although a stage-structured model would better capture this variation, our model structure is more suitable for our goal of comparing competition dynamics between the perennial *Stipa* and its annual competitor.

PARAMETER ESTIMATION

We combined data from nitrogen (N) gradient and density experiments with observational field data to parameterize each demographic model under three levels of N (Table 1). We used maximum likelihood with a lognormal distribution to estimate each model parameter from the data. We fitted all models in R v3.2.2 using nlsLM() from package('minpack.lm'). Data to fit all terms for the *Avena* seed model and *Stipa* seedling survival and competition terms came from a reciprocal invasion experiment we conducted at the South Coast Research and Extension Center for *A. fatua* and *Stipa* under three N levels (low, moderate, and high). We decreased soil N using table sugar at a rate of 421 g C m^{-2} year^{-1}. In similar sites, this level of carbon addition decreased inorganic N by about 30% (Cleland, Larios & Suding 2013). We increased N at a rate of 6 g N m^{-2} year^{-1}, which we applied in the form of slow-release calcium nitrate (Florikan®, Sarasota, FL). This supply rate followed the predicted N deposition rates for grassland systems to hit their critical N loads (Fenn *et al.* 2010). The moderate N treatment was ambient soil N. The soil amendments were done from 2009 to 2011 and were applied in three rounds during the winter (December–February) directly before a rainstorm. Data to fit *Stipa* germination and adult seed production came from a similar reciprocal invasion experiment with the same N manipulations conducted at the Irvine Ranch National Landmark (Irvine, CA). Data to fit the *Avena* germination, recruitment, and recruitment intraspecific competition terms

Table 1. Parameter estimates for *Avena* and *Stipa pulchra* population models under three levels of nitrogen (N). Details on experimental design and model structure for each experiment are presented in Appendix S1

Species/model	Parameter	Low N Estimate	Moderate N Estimate	High N Estimate	Data source
Avena					
Adults	g_a	0.73 ± 0.04	0.73 ± 0.04	0.73 ± 0.04	Dyer, Fenech & Rice (2000)
	r_a	1.29 ± 0.14	1.29 ± 0.14	1.29 ± 0.14	Exp. 3: SFREC
	α_{aa}	0.0016 ± 0.00037	0.0016 ± 0.00037	0.0016 ± 0.00037	Exp. 3: SFREC
Seeds	λ_A	-2.76 ± 0.61	11.5 ± 24.6	5.00 ± 4.79	Exp. 1: SCREC
	α_{AA}	-0.025 ± 0.0056	0.58 ± 1.3	0.037 ± 0.044	Exp. 1: SCREC
	α_{AS}	0.057 ± 0.056	-1.17 ± 1.76	-0.31 ± 0.11	Exp. 1: SCREC
	α_{As}	-0.080 ± 0.039	0.12 ± 0.28	-0.040 ± 0.044	Exp. 1: SCREC
Stipa pulchra					
Seedlings	p_p	0.31 ± 0.014	0.31 ± 0.014	0.31 ± 0.014	Exp. 4: Vasco Caves
	λ_P*	7.59 ± 0.68	7.59 ± 0.68	7.59 ± 0.68	Exp. 2: IRNL and Exp. 4: Vasco Caves
	α_{PP}	0.80 ± 0.14	0.80 ± 0.14	0.80 ± 0.14	Exp. 4: Vasco Caves
	r_p	0.052 ± 0.012	0.052 ± 0.012	0.052 ± 0.012	Exp. 2: IRNL
Adults	s_p	1.07 ± 1.45	0.36 ± 0.19	0.22 ± 0.059	Exp. 1: SCREC
	α_{pp}	0.09 ± 0.23	-0.069 ± 0.016	-0.14 ± 0.012	Exp. 1: SCREC
	α_{pA}	0.13 ± 0.37	-0.0095 ± 0.065	0.043 ± 0.024	Exp. 1: SCREC
	s_P	0.73 ± 0.043	0.73 ± 0.043	0.73 ± 0.043	Exp. 4: Vasco Caves

*Values are based on log transformed data to improve model fit.

came from a density gradient experiment we conducted at the Sierra Foothills Research and Extension Center (Browns Valley, CA), where we seeded the congener *A. barbata* on a scale from 32 to 3200 seeds per m^2 and followed its recruitment (Note: all other terms were fitted with data from *A. fatua*). Data to fit *Stipa* seed production, probability of reproduction, and adult survival terms came from a multi-year demographic observational study we conducted at Vasco Caves Regional Park (Livermore, CA), where we followed recruitment, growth, and survival and fecundity of *Stipa* individuals. The number of reproductive adults and fecundity data were log transformed to improve model fit. Any terms that were estimated from either the SFREC or Vasco Caves studies, which were not done along a resource gradient, we held constant across the three N treatments. These studies are described in detail in Appendix S1, Supporting Information. Additionally model fits are listed in Fig. S1, and all parameter estimates are listed in Table 1.

MODEL ANALYSIS

To evaluate whether *Avena* and *Stipa* dominated grasslands represent separate states, we used model parameters to simulate the outcome of competition between *Stipa* and *Avena*. We first allowed each species to equilibrate in the absence of interspecific competition. We then introduced the focal invader (note we use 'invader' here to indicate the species at low abundance, it could either be exotic or native depending on starting conditions) at a low density and simulated community change over the following 500 years. Low abundances were 1 individual for *Avena* and 0.1 adults for *Stipa*. We calculated the invading species' growth rate when rare (GRWR) and its equilibrium population size. For *Avena*, GRWR was calculated as the ratio of its population size at time $t + 1$ and time t. Because we are simulating population size for two life stages of *Stipa* – seedlings and adults – we created a matrix describing the transition between seedling and adult and calculated GRWR as the dominant eigenvalue of the matrix of transitions rates between these two life stages (Mordecai 2013;

Mordecai *et al.* 2015). The communities would be considered separate states if the invader could not increase when rare, while the other species is at equilibrium. Conversely if an invader could increase when rare, it would be evidence of coexistence and not separate states (Chesson 2000). To evaluate whether these communities' dynamics are susceptible to changes in N and/or exhibit hysteresis, we repeated this simulation under three different N scenarios (low, moderate, high). We varied parameter estimates when possible for the three different N scenarios (Table 1). We would infer hysteresis if both community states were able to resist invasion under the same N scenario such that the dominant community state was determined by initial starting conditions. Any changes in the invasion scenarios under the different N scenarios would be indicative of vulnerabilities to N enrichment for either the exotic or native state.

To link these model dynamics to potential management strategies, we additionally ran sensitivity analyses for each invasion simulation under each N scenario. We calculated sensitivity by individually increasing and decreasing the value of each parameter by 2% and then calculating the proportional change in GRWR and equilibrium population size (when allowed to equilibrate for 500 years).

Results

We observed from our models that both *Avena* and *Stipa* grasslands could persist but this persistence was dependent on N inputs (Fig. 1). Under low N, *Stipa* dominated conditions regardless of starting conditions: *Stipa* communities could resist invasion by *Avena* and *Stipa* could invade *Avena* communities (Fig. 1a,d). Under moderate-N conditions, we observed a hysteresis effect where initial conditions mattered: *Stipa* communities could resist invasion by *Avena* (Fig. 1b), while *Avena* communities shifted to mixed communities (dominated by *Avena* with *Stipa* able to coexist at low abundance) when *Stipa* was allowed
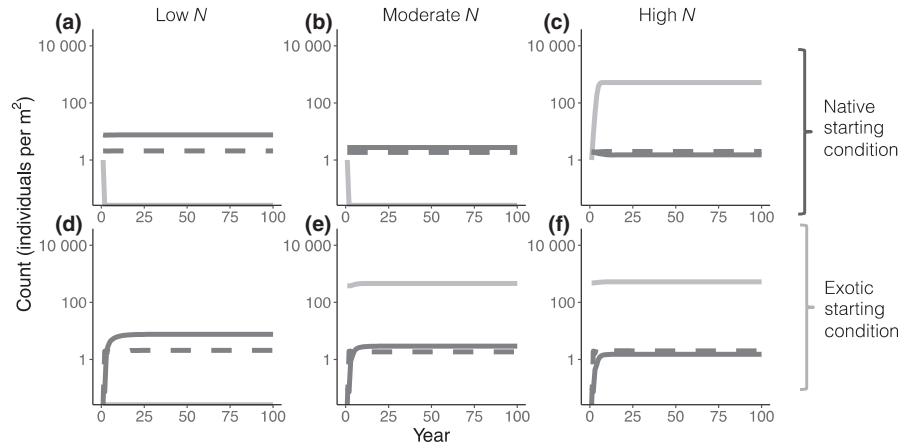
Fig. 1. Results of a demographic model, which assesses the density of two interacting species, exotic *Avena* (light grey) and native *Stipa* (dark grey; straight lines indicate adults, dashed indicates seedlings) at three different levels of nitrogen and at two different starting conditions (*Stipa* grassland a–c, *Avena* grassland d–f). In each plot the resident species initially is at equilibrium and the invader is introduced at low abundance at time step 0. Within-season dynamics are not shown; data represents population size at peak biomass in the spring. We present the first 100 years of the 500 year simulation due stable dynamics developing quickly.

to invade (Fig. 1e). Lastly, at high N inputs, *Avena* always maintained dominance, although *Stipa* was able to persist at a low abundance: *Avena* could always invade *Stipa* communities and *Avena* communities were always dominated by *Avena* (Fig. 1c,f).

As expected in a comparison of an annual and perennial species, model outcome sensitivity was affected by different demographic parameters for the two species. *Stipa* GRWR was most strongly influenced by per capita seed production (λ_P), such that an increase in fecundity in the absence of competition led to greater GRWR. In addition, increasing either the probability of adult reproduction (p_P) or the rate of seedling recruitment (r_p) increased GRWR (Fig. 2). These patterns were consistent across N conditions, and decreasing parameter values by 2% led to results of similar magnitude but opposite in direction. *Stipa* seedling and adult equilibrium population sizes were highly sensitive to per capita seed production (λ_P). Equilibrium population was more sensitive to intraspecific *Stipa* adult competition on seed production (α_{PP}) compared to GRWR. Additional parameters also affected *Stipa* equilibrium populations. For example, *Stipa* adult equilibrium was also highly sensitive to seedling and adult summer survival (s_p and s_P), where increasing survival increased population size. While these effects were consistent across N scenarios for *Stipa* adults, they varied for *Stipa* seedlings, such that adult survival benefited population size only at low N (Fig. 2).

For *Avena*, sensitivity tests were similar across moderate and high N conditions for equilibrium population size. However, at lower N levels, *Avena*'s negative per capita seed production (λ_A) resulted in *Avena* never establishing an equilibrium population. Consequently, we only present sensitivities for the moderate and high N model. Effects on *Avena* GRWR differed between moderate and high N scenarios. At moderate N, *Avena* GRWR was very

sensitive to interspecific competition from *Stipa* adults (α_{AP}), where increasing interspecific competition decreased GRWR. In contrast at high N, increases in per capita seed production (λ_A) and recruitment (r_a) had the largest effect on *Avena* GRWR (Fig. 3). *Avena* equilibrium population size was less affected by per capita seed production (λ_A) but remained sensitive to recruitment (r_a) under high N. *Avena* equilibrium population size was also highly influenced by intraspecific competition (α_{aa}), where an increase in α_{aa} decreased equilibrium population size (Fig. 3). Decreasing parameter values by 2% again lead to results of similar magnitude but opposite in direction.

Discussion

In the face of environmental change, managers increasingly need to anticipate and better understand resilience in both time (as environments change) and in space (across heterogeneous landscapes that are differentially exposed to change). These needs apply both to the conservation of native-dominated areas and the restoration of invaded areas. Our results yield basic predictions that can form the basis of management guidelines that look forward to future conditions of N inputs to better determine where two management challenges – conservation of native grasslands and restoration in exotic grasslands – should be best prioritized. We detail four management strategies that stem from our results and are generally applicable to the management of complex landscapes in the face of environmental change.

CONSIDER NATURAL RECOVERY: DO NOT INTERVENE UNLESS NECESSARY

There is much debate about how to identify whether a degraded system is 'stuck' and in need of intervention or whether a degraded system is disturbed and, given time,
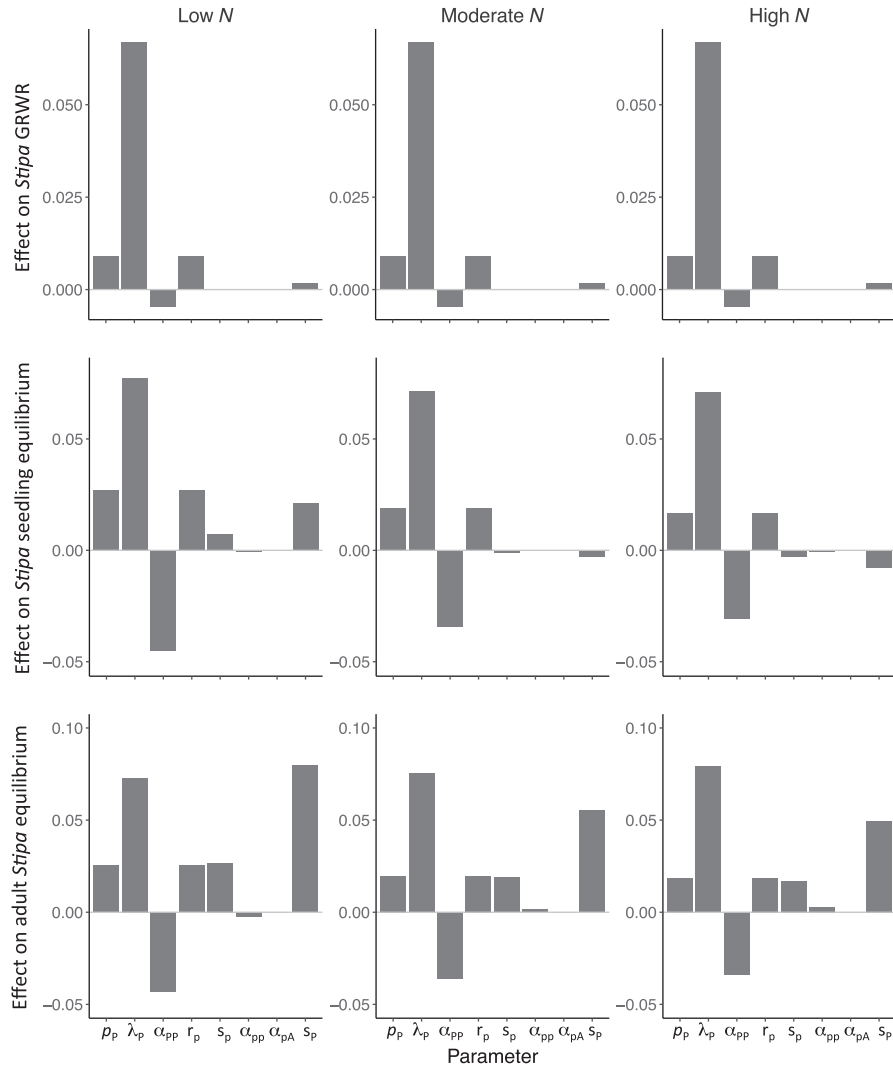
Fig. 2. Analysis of the sensitivities of growth rates when rare (GRWR) for *Stipa* invading *Avena* and single-species equilibrium population sizes of *Stipa* seedlings and adults at three levels of nitrogen (N) given a 2% increase in parameter values (sensitivities to a 2% reduction were of similar magnitude and opposite direction). Parameters are probability of adult reproduction (p_P) adult fecundity in the absence of competition (λ_P), the effect of adult intraspecific competition on fecundity (α_{PP}), seedling recruitment rate (r_p), seedling survival rate in the absence of competition (s_p), the effects of intra and inter-specific competition on recruitment (α_{pp} and α_{pA}) and adult summer survival (s_P). Subscripts *P, p, A* represent adult *Stipa*, seedling *Stipa* and *Avena* individuals respectively.

will follow a successional recovery trajectory (Holl & Aide 2011; Prach & Walker 2011). Although there is considerable social pressure for managers to intervene and do something in degraded areas, this distinction is important: active restoration is not always necessary, it costs considerable time and labour, and can result in unintended consequences (Holl & Aide 2011; Chazdon 2014).

An integrative approach such as the one we employ here can identify baseline conditions where resilience of the degraded area is low and natural recovery should be expected (Fig. 4). In the case of California grasslands where *Avena* and *Stipa* co-occur on a landscape, our results predict that *Avena* grasslands in low N areas are unlikely to persist without repeated disturbance, and will be replaced by *Stipa* given enough time. Due to variability

in our data for *Avena* at low N, we had difficulty modelling *Avena* in this scenario and more measurements would be helpful to reduce the uncertainty in our models. Under low N conditions, *Stipa* has a high GRWR that allows it to establish in *Avena* grasslands, a pattern that likely reflects Stipa's superior resource tolerance (Dyer & Rice 1999; Hamilton, Holzapfel & Mahall 1999). Positive density dependence is also apparent: the per-capita growth rate of *Stipa* increases as it becomes more abundant, allowing for competitive dominance and the exclusion of *Avena*. This positive density dependence likely reflects a positive feedback, and in the case of *Stipa,* could be due to feedbacks with the soil microbial community or species effects related to resource cycling (Hull & Muller 1977; Hawkes *et al.* 2005; Larios & Suding 2015).
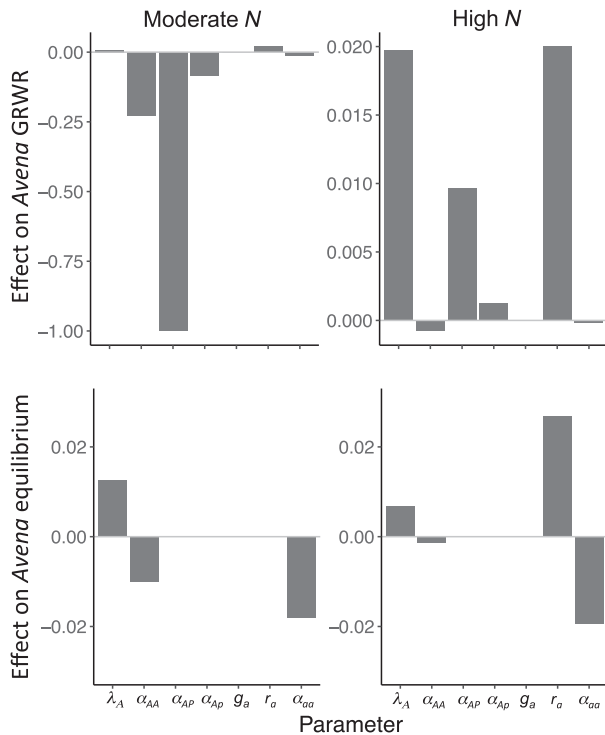
Fig. 3. Analysis of the sensitivity of growth rate when rare (GRWR) and single-species equilibrium population size of *Avena* under moderate and high nitrogen (N) conditions given a 2% increase in parameter values (sensitivities to a 2% reduction were of similar magnitude and opposite direction). Parameters are *Avena* fecundity in the absence of competition (λ_A), the effect of intraspecific and interspecific competition on fecundity (α_{AA}, α_{AP}, α_{Ap}), seed germination rate (g_a), seedling recruitment rate in the absence of competition (r_a) and the effect of intraspecific competition of seedling recruitment (α_{aa}). Subscripts *P, p, A* and *a* represent adult *Stipa*, seedling *Stipa* and *Avena* individuals at peak biomass and *Avena* germinants respectively.

While passive restoration may be the best management option in many systems (De Steven, Sharitz & Barton 2010; Holl & Aide 2011), a temporal mismatch between the time scale of recovery and time scale of human decision-making can make this option difficult to justify to stakeholders. In our study system, different life histories of the native and exotic make the decision even harder, as the long-lived native is expected to have much slower population dynamics than the short-lived annual grasses. While monitoring to assess trajectories of change is critical, they are best combined with models that project into the longer term future to evaluate the potential for slow – but unassisted – natural recovery. For instance, some outcomes in our model were only fully apparent after 50 years – too long to ask the public to wait for assurance that the project is meeting restoration goals. It also may be important to accept the need (either ecologically or socially) for intervention to speed a process that would otherwise occur more slowly without intervention (Hobbs *et al.* 2007; Holl & Aide 2011).

DON'T RESTORE EVERYWHERE: ACTIVE RESTORATION IS BEST EMPLOYED SELECTIVELY

Accompanying the decision about when to allow natural recovery without intervention is the decision about how best to allocate efforts directed at more active restoration (Hobbs & Cramer 2008; Holl & Aide 2011; Suding 2011). Managers can intervene in many ways to facilitate recovery, including earthmoving to affect topography and river channelization, reintroducing plants by adding propagules or plantings, changing soil conditions through topsoil removal or amendments, and influencing disturbance regimes such as fire or flooding frequency (Corbin & Holl 2012; Larios & Suding 2013; Palmer, Hondula & Koch 2014). While prioritizing schemes often include the extent of degradation and the proximity of native core areas (Cipollini, Maruyama & Zimmerman 2005; Thomson *et al.* 2009), they rarely incorporate environmental baselines that may influence the success of projects (Dickens *et al.* 2016).

Situations of hysteresis, where similar environmental conditions can support the persistence of two or more states, are cases where active restoration may be essential to the ensure successful restoration (Suding, Gross & Houseman 2004; Firn, House & Buckley 2010). In our study, we found evidence of hysteresis only at intermediate N-levels; at these baseline conditions, native *Stipa* grasslands were able to persist and resist invasion by *Avena* and – at the same baseline conditions – exotic grasslands were also able to persist and resist the invasion of *Stipa* (Fig. 4c). A high priority for active restoration would be invaded areas that occur in an environment that could maintain a restored state; in the case of our study, these high priority areas would be *Avena* invaded grasslands receiving intermediate N inputs.

Hysteresis dynamics are important to identify because they indicate that restoration focused on feedbacks and interactions should be an effective and sustainable management strategy (Suding & Hobbs 2009). Our observed hysteresis dynamics point to the need for restoration actions that establish positive feedbacks and jumpstart positive density-dependent growth that is evident in native grasslands. Because we suspect these feedbacks reflect plant–soil interactions, approaches could include intensive high-density plantings of *Stipa* in association with the addition of native soil microbial community innocula. Breaking feedbacks associated with *Avena* dominance (e.g. reducing *Avena* propagule pressure, for instance, Larios, Aicher & Suding 2013) may also be effective to reduce the resilience of *Avena* and shift the system to one where *Stipa* feedbacks predominate. Reducing N inputs or the cumulative N amounts may be an third option at these intermediate N levels, as a reduction in N might push the system to dynamics more similar to those we find at low N.

While hysteresis dynamics should help prioritize areas where active restoration may be most effective, these
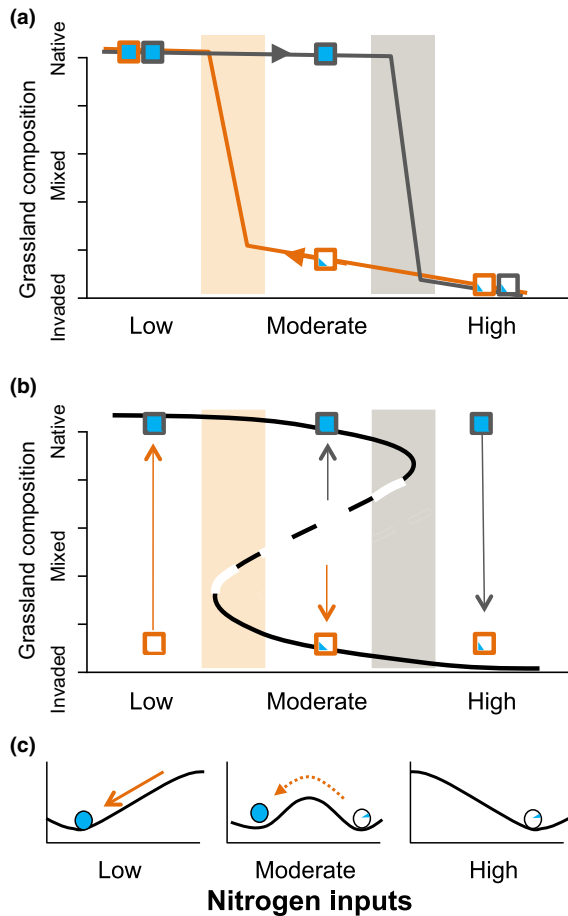
Fig. 4. Predicted composition of native (blue filled symbols) and invaded (open symbols) grasslands from model results (at *T* = 100; Fig. 1) across N inputs. (a) Starting conditions (*Avena*-orange, *Stipa*-grey lines) do not affect equilibrium composition at high or low N inputs, with evidence of hysteresis at moderate N inputs. The shaded areas indicate zones of critical transitions, where the transition from *Avena* to *Stipa* (the restoration scenario) occurs between moderate and low N levels, while the transition from *Stipa* to *Avena* (the invasion scenario) occurs between moderate and high N levels. Coexistence occurs at moderate N (partially filled symbol), where *Stipa* is able to invade and persist at low abundance. (b) Translation of results in (a) to show possible stable equilibria (black line) and unstable equilibria (dashed line, at moderate N region). Arrows depict expected trajectories from starting conditions. (c) Ball and cup diagrams where attractors are shown as valleys where the system (the ball) will travel to with little intervention. The two valleys at moderate N levels indicate a situation of hysteresis, and the importance of starting conditions. Passive restoration through natural recovery is shown by the solid orange arrow at low N levels, while active restoration (dashed arrow) is required to push the invaded state to a more native state at moderate N levels. Persistence of a native state at high N would not be self-sustainable.

dynamics are notoriously difficult to identify (Schroder, Persson & De Roos 2005; Andersen *et al.* 2009; Thrush *et al.* 2009). We were able to infer where these dynamics may occur using experimental results that assess population growth across different environmental conditions in degraded and native starting conditions. A modelling

approach was important to tie these short-term experimental results to longer term population dynamics and ultimately compositional trajectories. The incorporation of environmental change factors in addition to N would improve the generality of these results to management concerns; for instance, the effects of N inputs may be additionally mediated by changes in rainfall (Harpole, Potts & Suding 2007; Everard *et al.* 2011). In the absence of associated sharp environmental discontinuities, threshold patterns can also be discerned by time-series analyses, indicated by abrupt transitions over time, or spatial analyses, indicated by sharp boundaries (Andersen *et al.* 2009; Bestelmeyer *et al.* 2011).

It is important to note that this approach will almost always necessitate a collaborative strategy between land managers and scientists, as it requires both strong empirical field data, as well as technical expertise. We encourage managers who can help frame the question to work alongside researchers with modelling expertise who can inform and help prioritize data collection and conduct the technical modelling. We view this as an iterative process to ensure that results are usable for managers and assumptions align with natural history and tools available on the ground.

REMNANT AREAS APPROACHING A TRANSITION NEED SPECIAL CARE, OTHERS SHOULD BE LEFT ALONE

As land managers have little ability to control regional- and global-scale environmental changes, a hands-off approach aimed at protecting conservation areas from threats and disturbance is being replaced with active management to increase the resilience of these areas (Bengtsson *et al.* 2003; Baron *et al.* 2009). However, it has been challenging to determine when intervention is needed in existing high value conservation areas, as actions can also disrupt processes and the network of interactions that have allowed conservation remnants to persist (Larios & Suding 2013).

Resilience theory would suggest that interventions are best prioritized in areas nearing a critical transition (Suding, Gross & Houseman 2004; Thrush *et al.* 2009). In our study system, different approaches are likely needed to conserve native grasslands depending on N inputs. Native grasslands appear to be resilient at low N; invasions after a perturbation should be transient and not result in a conversion to exotic grassland. However, as N inputs increase to moderate levels, resilience depends on how perturbations affect the abundance of *Stipa*. Low intensity disturbances may result in similar transient invasion dynamics as long as adult survival and fecundity is not greatly affected. However, a disturbance that is severe enough to kill *Stipa* adults and allow the establishment of *Avena* can shift basins of attraction towards an *Avena* state where *Stipa* is not able to reinvade, as *Stipa* populations rely primarily on adult survival than an intact seedbank to buffer population size (Mordecai *et al.* 2015). These

dynamics likely occur during type conversions following severe fires (Larios, Aicher & Suding 2013), and suggest that practices that protect remnants from severe disturbances should be high priority for these areas.

Assessing early warning indicators for an approaching critical transition has been a subject of much recent work (Scheffer *et al.* 2012; Dakos *et al.* 2015). As we conducted simulations for three levels of N inputs, we are only able to infer that the critical transition between vulnerability to a state change and more stable persistence occurs between our low and moderate N-input levels. We expect that the critical threshold varies based on many other factors which influence soil biogeochemistry and nutrient availability at a site (Hoopes & Hall 2002; Parker & Schimel 2011), and may be beyond the scope of demographic models such as the one we use here.

SUCCESS IS CONTEXT DEPENDENT: ENVIRONMENTAL CHANGE MAY MANDATE A CHANGE IN MANAGEMENT GOALS

With the rapid rates of environmental change, management goals must reflect that shifting baselines may affect the potential of areas to support particular habitat types or species (Choi *et al.* 2008; Hobbs & Cramer 2008). While management goals may need to reflect a new reality given future change, there is debate about how to determine when these goals should deviate from more conventional restoration references (Seastedt, Hobbs & Suding 2008; Hobbs *et al.* 2014; Murcia *et al.* 2014). A modelling framework is one quantitative solution that allows the exploration of potential outcomes across environmental conditions.

Assessing the potential conservation and restoration alternatives is an essential step to assess what restoration goals are suitable in a given environmental context (Suding *et al.* 2015). In our study, we find restoration in areas receiving high-N inputs is risky, as we find that the invaded state dominated by *Avena* has high resilience. Population dynamics in these areas indicate that restoration by reintroduction of *Stipa* at any density is not likely to be successful because it has low population growth rates regardless of its density. We suspect this shift is indicative of increased growth by *Avena* due to increased N availability, which then reduces light levels (Dyer & Rice 1999). High N areas might be candidates for less traditional restoration options, such as restoration of native forbs with faster growth rates that may be able to compete with *Avena* (Hobbs *et al.* 2014).

Conclusions

While applying resilience theory to better understand and anticipate environmental change has been challenging, we show how demographic modelling approaches are one way to assist in decision making given future uncertainty. Using a modelling framework that takes into account species interactions in different environmental conditions and with different starting conditions, we yield basic predictions that can be used to help anticipate and better understand how a widespread environmental change, increasing inputs of N deposition, may affect the conservation and restoration of native grasslands in California. Restoration decision-making has often not incorporated quantitative modelling (Failing, Gregory & Higgins 2013), yet these tools are well-suited to address the need to forecast complex dynamics under future scenarios (McBride *et al.* 2010). This approach will require strong collaborative efforts between land managers and scientists, which has been very successful in conservation science, where these partnerships have promoted the integration of quantitative techniques into decision making (e.g. Guisan *et al.* 2013; Tarrant & Armstrong 2013). We encourage further thought on how best to establish these partnerships at the local level and encourage further collaboration with monitoring program design as well as process-based experimental assessments of mechanisms. This combined collaborate approach that capitalizes on both field data and the quantitative synthesis of these data will inform how best to allocate limited management resources as baselines shift: where natural recovery is possible, where best to allocate active restoration efforts, and where native remnants may be most vulnerable.

Authors' contributions

Acknowledgements

Data accessibility

Data are available via Dryad Digital Repository https://doi.org/10.5061/dryad.7qj20 (Larios, Hallett & Suding 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Summary of model fits.

Appendix S1. Data sources and experimental design supplement.