**LETTER**

# Niche opportunities and invasion dynamics in a desert annual community

Ginger R. H. Allington,[1]* David N. Koons,[2] S. K. Morgan Ernest,[3] Michele R. Schutzenhofer[4] and Thomas J. Valone[1]

## Abstract

Although many factors influence the ability of exotics to invade successfully, most studies focus on only a few variables to explain invasion; attempts at theoretical synthesis are largely untested. The niche opportunities framework proposes that the demographic success of an invader is largely affected by the availability of resources and the abundance of its enemies. Here, we use a 31-year study from a desert ecosystem to examine the niche opportunities framework via the invasion of the annual plant *Erodium cicutarium*. While the invader remained rare for two decades, a decline in granivory combined with an ideal climate window created an opportunity for *E. cicutarium* to escape control and become the dominant annual plant in the community. We show that fluctuations in consumption and resources can create niche opportunities for invaders and highlight the need for additional long-term studies to track the influence of changing climate and community dynamics on invasions.

## Keywords

Community reorganisation, competition, exotic species, *Erodium cicutarium*, granivory, rodents.

*Ecology Letters* (2013) **16**: 158–166

## INTRODUCTION

Invasion of native ecosystems by non-native species is an increasingly common threat to biodiversity worldwide (Vitousek *et al.* 1996; Butchart *et al.* 2010). Although many factors influence the ability of exotics to invade successfully (Cushman *et al.* 2011), most studies to date focus either on individual traits of the invading species (Rejmanek & Richardson 1996; Seabloom *et al.* 2003; Hill & Kotanen 2009) or on particular aspects of a community that might make it more prone to invasion (Davis *et al.* 2000; Levine 2000). While there have been several attempts to propose a unified hypothesis for invasion, these are largely catalogues of the various characteristics identified in previous studies (Catford *et al.* 2009; Perkins *et al.* 2011).

A simple unified conceptual framework for invasions was proposed a decade ago by Shea & Chesson (2002) based on the concept of 'niche opportunities'. In the niche opportunities framework, the demographic success of an invader is largely affected by the availability of resources and the abundance of its enemies, either competitors or consumers. Niche opportunities for invaders are hypothesised to occur when resource levels are high and/or enemy populations are low. Therefore, large fluctuations in either resources (Davis *et al.* 2000; Bradley *et al.* 2010) or the populations of competitors or consumers (Shea & Chesson 2002; Schoolmaster & Snyder 2007) can create conditions conducive to invasion.

While the niche opportunities framework provides a unique community ecology perspective from which to view invasions, it has been largely untested. This is likely due to two reasons. First, long-term data are needed to capture the kinds of fluctuations that would create such an opportunity, and most experiments on invasions occur over relatively short timescales (e.g. see Appendix S1 in Supporting Information). Second, although Shea and Chesson outline the conditions that must be met to create a niche opportunity, they do not propose explicitly testable predictions that could be used to devise empirical tests. However, because the conceptual basis is very clear, it is possible to develop testable predictions from their framework. Based on the reasoning outlined by Shea & Chesson (2002), one can predict that for a niche opportunity to occur (1) the efficiency or abundance of natural enemies must decrease over time and/or (2) limiting resources must become more available to the invader. Therefore, to demonstrate that an invader is taking advantage of a niche opportunity, one must first demonstrate that the invader's abundance is either (i) regulated by one or more natural enemies or (ii) limited by resources. It must also be demonstrated that as these enemies decline in abundance or effect, or as resources increase, the abundance of the invader increases. All of this requires long-term data.

Here, we use a 31-year study from a desert ecosystem in southwestern North America to examine the niche opportunities framework. At this site, the winter annual plant community has been invaded by the exotic species *Erodium cicutarium,* a large-seeded annual introduced to North America from the Mediterranean (Kearney & Peebles 1960; Mensing & Byrne 1998). In an independent study conducted at this site, *E. cicutarium* was shown to competitively suppress native annuals (Schutzenhofer & Valone 2006). Schutzenhofer & Valone (2006) documented lower native annual plant abundance in years of high *E. cicutarium* abundance over 16 years of data, and an increase in native abundance and richness at the quadrat level after experimental removal of *E. cicutarium* over 1 year (Schutzenhofer & Valone 2006). Despite being a strong competitor, *E. cicutarium* remained a rare species in the community for 20 years

[1]*Department of Biology, Saint Louis University, St. Louis, MO, 63103, USA*
[2]*Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, 84322, USA*
[3]*Department of Biology and the Ecology Center, Utah State University, Logan, UT, 84322, USA*

[4]*Division of Science & Mathematics, McKendree University, Lebanon, IL, 62254, USA*
*Correspondence: E-mail: gallingt@slu.edu*
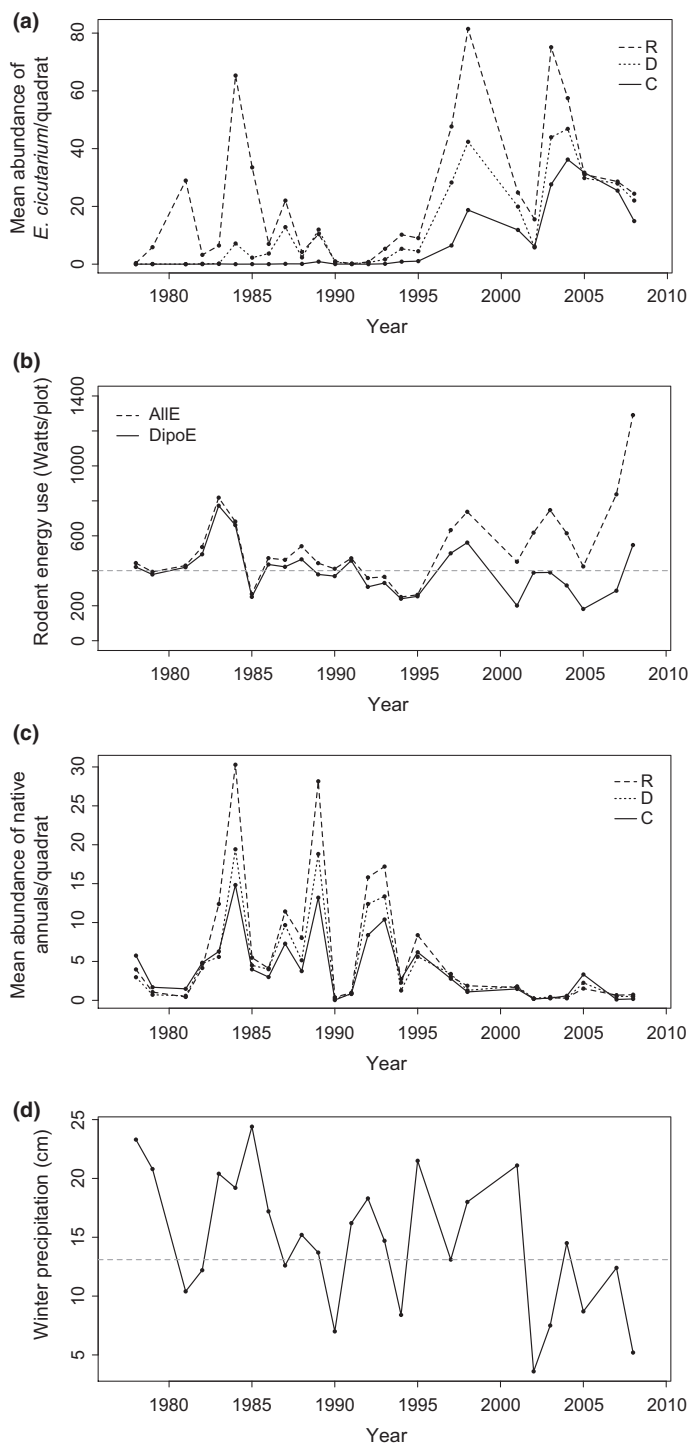
**Figure 1** Response and predictor variables. (a) Mean abundance of *E. cicutarium* per quadrat. (b) Mean energy use by *Dipodomys* (DipoE), and all rodents (AllE) on control plots. Estimated individual metabolic rates were summed on each plot for all individuals captured, and then averaged by the number of months of data collected in that year. (c) Mean abundance of annual plants per quadrat on rodent removal (−R), *Dipodomys* removal (−D) and control (C) plots. (d) Total winter precipitation (October through March of the year noted) measured on the site; totals for 1997 and 2003 are estimated based on data collected 10 km from the site. Light grey lines in (b) and (d) represent 31-year mean. Years 1980, 1990, 1996, 1999, 2000, 2006 were dry with extremely low abundance of nearly all annuals and were not included.

(Fig. 1a) before it rapidly increased in abundance. Given that (1) *E. cicutarium* has a large seed that is a target of rodent seed predation (Samson *et al.* 1992; Schiffman 1994; Brock & Kelt 2004), (2) both annual plant species and rodent populations at the site experience strong fluctuations in abundance due to stochastic variation in precipitation (Brown & Heske 1990; Ernest *et al.* 2000), and (3) precipitation is a limiting resource in arid ecosystems that limits plant growth and reproduction and can influence competition among annual plants (Chesson *et al.* 2004), it is possible that the sudden increase in this invader after 20 years could be attributed to niche opportunities. As such, this is an ideal system to test predictions based on the niche opportunity framework (Shea & Chesson 2002).

To demonstrate that the invader is susceptible to natural enemies, we document that *E. cicutarium* first invaded plots that have been subjected to the experimental removal of granivorous rodents. We then use 31 years of data on plants, rodents and precipitation to explore the effects of fluctuations in rodents (consumption), precipitation (resource fluctuation) and the abundance of native annuals (potential competition) on the abundance of *E. cicutarium*. Finally, we examine how the invasion and ultimate dominance of the invader negatively affected the native annual plant community.

## MATERIAL AND METHODS

### Study system and experimental design

Data come from the Portal Project, a 20-ha Chihuahuan desert scrubland site in the San Simon valley in southeastern Arizona (Brown & Munger 1985; Valone *et al.* 1995). Climate at the site is characterised by a bimodal distribution of precipitation, with distinct summer (July–September) and winter (October–March) rainy seasons. This bimodality in precipitation results in two distinct annual plant communities (Samson *et al.* 1992). Because the invasive species is restricted to the winter annual community, we focus our analyses solely on that community.

The Portal Project was initiated in 1977, when 24 plots (50 × 50 m) were established at the site within a grazing exclosure. Plots are subjected to experimental treatments that include various combinations of the removal of granivorous rodents and ants (Brown & Munger 1985). Because the ant community is active only in the summer, we focus only on the rodent impacts on the plant community. In 1989, the treatments were reassigned on 12 of the 24 plots rendering them not useful for the current study. Instead, we use data from the 12 plots that have had the same experimental rodent treatments since 1977 (for details, see Brown & Munger 1985; Ernest *et al.* 2009). These include (1) four rodent removal plots that exclude all rodents (−R), (2) four plots that exclude three species of large-bodied kangaroo rats of the genus *Dipodomys,* but allow access by all other, smaller rodents (−D), and (3) four control plots that are accessible to all rodents (C). The treatments are highly effective. We capture (and remove) on average less than one rodent per treatment plot per month, while control plots average more than six individuals per plot per month (Ernest *et al.* 2009). Similarly, only a few kangaroo rats have ever been captured on *Dipodomys* removal plots (Brown & Munger 1985; Ernest *et al.* 2009).

Rodents are captured each month, around the new moon, by placing 49 Sherman traps (7.6 × 8.9 × 22.9 cm) on each plot for one night. Traps are baited with millet. Captured rodents are measured, weighed and identified to species and sex, uniquely marked

and their reproductive condition determined (for details, see Thibault *et al.* 2010). We restricted our analyses to the data on granivorous rodents as they are both the most abundant guild at the site and the most likely to impact annual plant dynamics. These species include representatives from both the Heteromyidae (*Dipodomys merriami, D. ordii, D. spectabilis, Chaetodipus baileyi, C. hispidus, C. intermedius, C. penicillatus, Perognathus flavus*) and the Muridae (*Baiomys taylori Peromyscus eremicus, P. leucopus, P. maniculatus, Reithrodontomys fulvescens, R. megalotis, R. montanus*).

Plants are censused on each plot during peak flowering of the annual plants (March–April) and all rooted plants within each quadrat are counted. Each plot contains 16 regularly spaced 0.25 m$^2$ quadrats that are censused twice annually (Samson *et al.* 1992). In 1978 and 1980–1982, eight of the 16 quadrats were censused in each plot. In 1979, four quadrats were censused in each plot.

## Explanatory variables for invasion

Using data from 1978, when *E. cicutarium* was absent on all but one plot (a −R plot), through 2008, when *E. cicutarium* was common on all plots, we examined the influence of rodent seed predators, native winter annual forbs, conspecific density and winter precipitation on *E. cicutarium* population dynamics. Because seed predation could limit the ability of an invasive plant to populate a new environment, we considered two parameterisations of rodent consumption pressure on seeds: the energy requirements for all rodents (AllE) or just the large-bodied *Dipodomys* rodents (DipoE) that prefer large seeds like those produced by *E. cicutarium*. Individual metabolic rates – an index of consumption demands of a rodent for seeds – were estimated using an allometric relationship relating the mass of an individual (M) with field metabolic rate in Watts (B): B = 5.69 M$^{0.75}$ (White *et al.* 2004). AllE and DipoE were then calculated for each plot for each month by summing across individual metabolic rates. This results in a monthly estimate of total granivorous rodent demands for energy, and thus seeds, on each plot. Since each year there is only one plant abundance value, these monthly rodent values were averaged from April of the year before germination through March of the year of germination to provide an estimate of the average seed predation pressure for the year leading up to winter annual germination. Because rodent energy variables can be calculated for each plot for each year, they could help explain both spatial and temporal variation in *E. cicutarium* abundance, whereas the treatment variables alone (described above) can only explain spatial differences.

While we know that *E. cicutarium* is competitively dominant over native plants (Schutzenhofer & Valone 2006), competitive interactions with native winter annual forbs could still impact the overall fitness of *E. cicutarium* and indirectly exert intraguild regulation of its abundance. Therefore, we incorporated the potential impact of the native forbs (at year *t* or *t*-1) by calculating for each quadrat the summed abundance (total number of individuals) of all non-*E. cicutarium* winter annual forb species. To examine intraspecific competition at the quadrat level, we also considered the effect of *E. cicutarium* abundance at year *t*-1 on abundance at year *t*.

Because of its limiting properties, precipitation is expected to be the dominant climatic driver of plant demography in arid and semi-arid environments (Thibault *et al.* 2010). Thus, we also considered the effect of winter precipitation (October–March) at our study area on winter *E. cicutarium* abundance. In the mid-1990s, major shifts in the El Niño Southern Oscillation (ENSO) and Pacific Decadal

Oscillation (PDO) occurred, which led to drastic changes in precipitation patterns and subsequent impacts on the ecosystem (Brown *et al.* 1997). After the shift, conditions were on average drier, and *Dipodomys* rodents became relatively rare (Brown *et al.* 1997; White *et al.* 2004). The DipoE variable described above captures this climate-driven shift in the ecosystem through its effects on *Dipodomys* species, but it could also explain variation in *E. cicutarium* abundance driven by indirect biotic and abiotic mechanisms.

Data files for plant abundance, rodent energy use and precipitation are available in the Dryad repository: doi:10.5061/dryad.3768m.

## Data analysis

Rather than transforming the count data, we analysed variation in *E. cicutarium* abundance at the quadrat level using discrete distributions naturally suited for numbers ≥ zero (O'Hara & Kotze 2010). Specifically, we developed stochastic population models with Gompertz density-dependence cast within the framework of generalised linear mixed models (GLMM). Using either a Poisson or negative binomial distribution and the log-link function, our models took the general form of

$$z_{j,t+1} = a + (b+1)z_{j,t} + \sum_i c_i x_i + \varepsilon_{j,t}, \qquad (1)$$

where $z_{j,t}$ is the log of *E. cicutarium* abundance in quadrat *j* and year *t*, *a* is an intercept, *b* is the coefficient of intraspecific density dependence, the $c_i$ are the coefficients for all other covariates $x_i$ (e.g. rodent energy requirements, densities of native winter annual forbs, precipitation), and $\varepsilon_{j,t}$ is a term for stochastic variation around the deterministic process. The lag one autocorrelation of the logged population abundance is $d = b + 1$ when the process is stationary. When $|d| < 1$, $z_{j,t}$ will approach a density-regulated stochastic equilibrium with a mean of

$$\left(a + \sum_i c_i x_i\right) / (1 - d)$$

and a variance of $\sigma^2/(1-d^2)$, where $\sigma^2$ is the temporal variance of $\varepsilon_{j,t}$ (Dennis *et al.* 2006; Creel & Creel 2009). Covariates for native or non-native abundance were always on the log scale (eqn 1) and all other covariates were standardised. Over the course of the study, *E. cicutarium* went from being extremely rare to becoming the dominant winter annual forb. There were also several years with extremely low precipitation which resulted in zero abundance of nearly all annual forbs. As a result, there was a high frequency of census counts equal to zero, prompting us to also consider zero-inflation models (Zuur *et al.* 2009).

Rather than examining the many possible combinations of explanatory variables, we used a tiered approach to identify the best explanatory model of spatial and temporal variation in *E. cicutarium* abundance (Franklin *et al.* 2000). We began by comparing zero-inflated negative binomial GLMs (random effects were added later) with alternative parameterisations of the same types of variables (e.g. the different rodent prevalence variables) using Schwarz's Information Criterion (SIC; Schwarz 1978, a.k.a. the Bayesian Information Criterion). A quadratic effect of the precipitation variable was also considered at this stage.

We then developed a global model that included additive and plausible interactive effects of the rodent prevalence, native winter annual forbs, conspecific density and precipitation variables that performed best in the preceding analyses. To determine whether a zero-

inflation parameter was needed and which distribution best fit the data (Poisson and 'NB1' vs. 'NB2' parameterisations of the negative binomial; Hilbe 2011), we compared alternative versions of the global model with these different statistical properties using SIC. Further analyses were then based on the best performing probability distribution and zero-inflation parameterisation (Bolker *et al.* 2009).

Next, we constructed a global GLMM by modelling $\varepsilon_{j,t}$ with crossed random effects; we included a nested random effect of 'quadrat within plot within treatment' to model random spatial variation among quadrats according to the nested study design (see Buckley *et al.* 2003), and a 'year' random effect to model temporal stochasticity. We then examined the need for including these random effects using likelihood ratio tests (Bolker 2008). After identifying the appropriate random-effect structure for the global GLMM, we proceeded by removing non-significant ($\alpha > 0.05$) fixed-effect parameters in a backwards-stepwise process until a model was found where all effects were significant and estimated precisely (Zuur *et al.* 2009).

Estimation of all GLMs and GLMMs was done using the 'glmmADMB' package (version 0.6.7.1) in R 2.14, which is currently the only statistical package that can accommodate zero-inflated negative binomial models with random effects (aside from custom-built programming code; Fournier *et al.* 2012). Moreover, this package estimates the maximum likelihood of parameters using Laplace approximation, which is more accurate than other algorithms that are commonly used to fit GLMMs (e.g. penalised quasi-likelihood; Bolker *et al.* 2009).

### Community composition

We evaluated the differences in native annual plant community abundance and richness on plots where *E. cicutarium* was present, using data from the 192 quadrats on the 12 treatment plots from 1978 to 2008. We focus on the quadrats because the small scale at which competition between annual plants occurs is better represented at the size of a quadrat (0.25 m$^2$) instead of at the larger plot scale (0.25 ha) (Schutzenhofer & Valone 2006). For each year, we divided the 192 local plant communities (quadrats) into two categories: those containing at least 10% *E. cicutarium* ('invader common') and those containing < 1% *E. cicutarium* ('invader rare'). Quadrats that had more than 1% but < 10% *E. cicutarium* were not included, to create a clear break point between categories.

To explore the relationship between the abundance or richness of natives and *E. cicutarium* prevalence, we plotted the mean abundance or richness of native annuals on a quadrat when *Erodium* was rare (x-axis), vs. when *Erodium* was common (y-axis). This yields one point for each year. By adding a 1 : 1 line, we can then assess the general trend in native abundance or richness with respect to *Erodium* presence. More points above the 1 : 1 line would indicate that natives were more abundant/exhibited greater richness when *E. cicutarium* was common, while more points below the line would indicate that natives were more abundant/exhibited greater richness when *E. cicutarium* was rare.

### RESULTS

### Invasion pattern

*Erodium cicutarium* increased dramatically on the study plots over time. In 1978, *E. cicutarium* was present on just one plot: 12

individuals were counted on adjacent quadrats of a rodent removal plot (Fig. 1; Table S2). From 1978 to 1982, *E. cicutarium* was only recorded on rodent removal plots; by 1984, it had been observed on all four rodent removal plots and all four *Dipodomys* removal plots. In contrast, the invader did not appear on a single control plot until 1983 (Fig. 1a). Following its delayed appearance on control plots, *E. cicutarium* remained rare and accounted for only a small fraction of the annual plant community on these plots; *E. cicutarium* comprised < 5% of the community on control plots for almost 20 years (Fig. 2a). After 1997, the fraction of the winter community on control plots represented by *E. cicutarium* rose rapidly (Fig. 2a), and by 2007, it had become the dominant species in the annual plant community and was present on nearly every quadrat (Fig. 2b). The increase in *Erodium cicutarium* on control plots was preceded by a decline in *Dipodomys* abundance in the early 1990s (Fig. 1b).

### Niche opportunity

Our initial analyses indicated that variation in *E. cicutarium* abundance was better explained by DipoE, lagged effects of both conspecific and native winter annual forb densities, and a quadratic
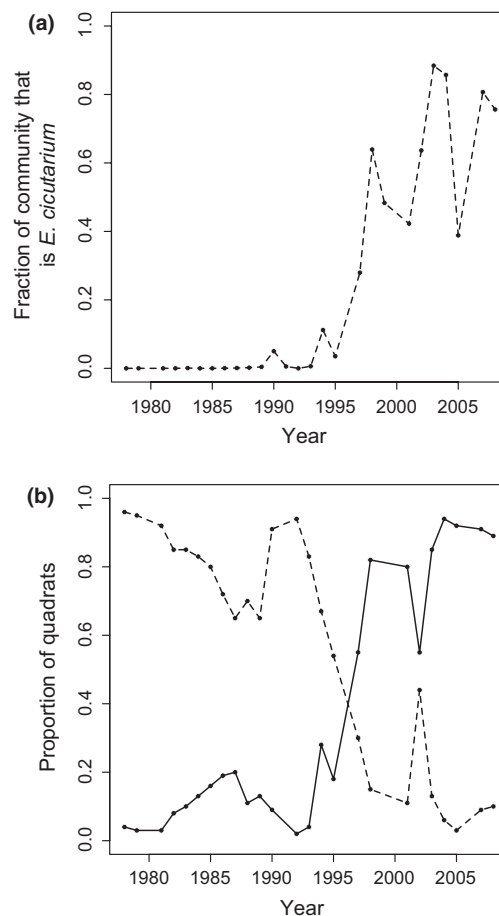
**Figure 2** (a) Mean fraction of the winter annual community on the four control plots that comprised *E. cicutarium*. Years 1980, 1990, 1996, 1999, 2000, 2006 were not included due to extremely low abundance of all annuals. (b) Proportion of the quadrats on which *E. cicutarium* was common (> 10% of individuals; solid line) or rare (< 1% of individuals; dashed line). Total number of quadrats censused was 48 in 1979, 96 in 1978, 1980–1982, and 192 in 1983–2008. Data for this panel are pooled across all three treatments.

effect of precipitation than other parameterisations of these biotic and abiotic effects on *E. cicutarium* dynamics (Table S3-1 in Appendix S3). Using these supported effects, we built a global model consisting of hypothesised interactions between DipoE and native winter annual forb density, DipoE and quadratic precipitation, native winter annual forb density and quadratic precipitation, as well as conspecific density and quadratic precipitation. Our comparison of different distributions and zero-inflation parameterisations for the global model indicated that the NB1 parameterisation of the negative binomial distribution provided a superior fit to our data and that zero-inflation needed to be accounted for (Table S3-2 in Appendix S3; zero-inflation parameter = 0.04, SE = 0.01).

Proceeding with these basal model properties, we then added the crossed random effects, which were both supported by the likelihood ratio tests (all $P < 0.01$; Table S3-3 in Appendix S3). After including the random effects, many of the fixed effects in the global GLMM were not significant ($P > 0.05$). We thus proceeded by removing non-significant effects, one at a time in a backwards fashion, until we found a model where all effects were significant. None of the interaction terms were supported, nor was the additive effect of native winter annual forb density (the estimated coefficient was negative ($-0.004$), indicative of interspecific competition, but was not significant: see Table S3-4 in Appendix S3).

With reference to equation one, our final GLMM included significant fixed effects of the intercept ($a = 1.49$, SE = GLM 0.40), intraspecific density dependence ($d = 0.13$, SE = 0.005), DipoE ($cDipoE = -0.20$, SE = 0.04) and a quadratic effect of precipitation ($c_{ppt} = 5.77$, SE = 1.69, $c_{ppt^2} = -4.63$, SE = 1.60). However, both dry and wet conditions strongly limited the ability of *E. cicutarium* to invade the native winter annual forb community (Fig. 3a). The energetic demands of *Dipodomys* rodents further expanded the zone of niche intolerance for *E. cicutarium* and moderated its population growth after invasion (Fig. 3b).

Other sources of environmental variability also had significant effects on *E. cicutarium* population dynamics at the Portal study area; the largest source of which was attributable to temporal stochasticity ($\sigma^2 = 3.64$ for the year random effect). Precipitation and *Dipodo-* *mys* energy requirements were generally good predictors of the observed *E. cicutarium* dynamics at Portal, but temporal stochasticity also limited *E. cicutarium*'s ability to invade and created an opportunity for it to increase (Fig. 4). There was also spatial variation among quadrats within plots ($\sigma^2 = 0.076$) and among plots within treatments ($\sigma^2 = 0.080$), which may have been attributable to underlying variation in soil quality and other localised factors that we did not measure. A lesser amount of unexplained variation existed across the treatments ($\sigma^2 = 0.046$).

### Community transformation

The increase in abundance of *E. cicutarium* was associated with reduced abundance and diversity of native annuals (Fig. 2). In most years, quadrats where *E. cicutarium* was abundant had lower abundance and/or richness of natives compared with plots in the same year with low *E. cicutarium* abundance (Fig. 5).

### DISCUSSION

We used a unique 31-year data set to explore the impact of consumption, competition and climate on the invasion of a non-native annual, *E. cicutarium*. Based on the niche opportunity framework proposed by Shea & Chesson (2002), we predicted that fluctuations in consumers or resources could create an opportunity for an exotic invader to escape biotic control. Our results indicate that both of these factors were crucial in creating a niche opportunity for *E. cicutarium* at the Portal site, as were stochastic events.

The impact of seed predation on the abundance of *E. cicutarium* was supported by our best-fitting statistical model, which showed a significantly negative relationship between the abundance of *E. cicutarium* and the energetic requirements of rodent granivores, particularly *Dipodomys* spp. When *Dipodomys* are removed from plots, *E. cicutarium* increases, and when *Dipodomys* consumption is low on controls, *E. cicutarium* increases (Fig. 3b). This supports the interpretation that declines in *Dipodomys* energy requirements in the mid-1990s (Fig. 1b) may have in part allowed for a rapid increase of
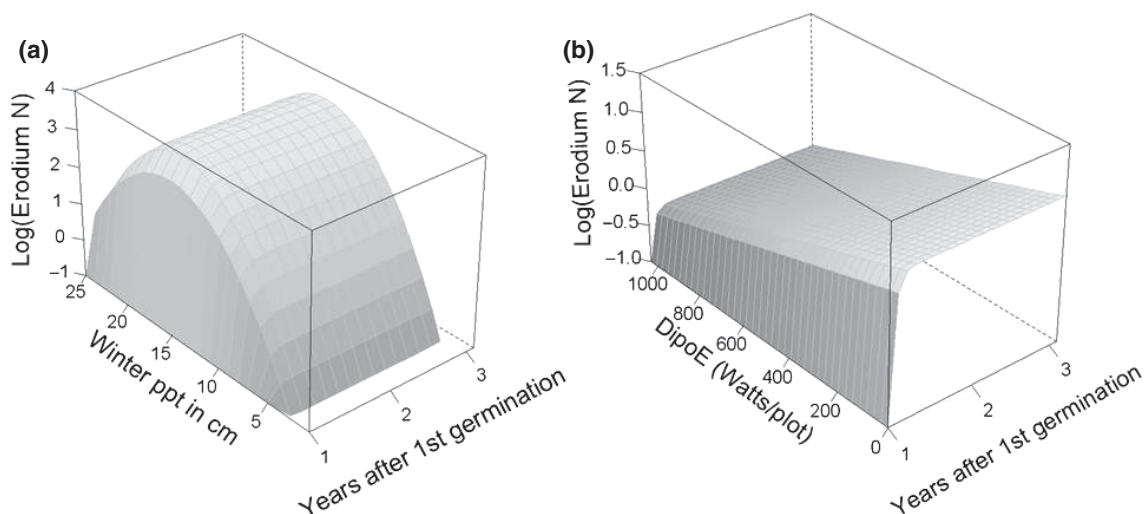


**Figure 3** Deterministic growth of *E. cicutarium* from low abundance up to the mean of its stochastic equilibrium. Panel (a) depicts the estimated effect of winter precipitation (ppt; evaluated at the overall mean of DipoE across all three treatments: 142.75 Watts/plot) on *E. cicutarium* population growth on a quadrat, and panel (b) depicts the effect of *Dipodomys* energy requirements (DipoE; evaluated at 7 cm of ppt; mean = 13.1 cm). If growth plateaus below log(1) = 0, *E. cicutarium* cannot invade under the given conditions, and if it plateaus below log(2) = 0.693, population growth is retarded.
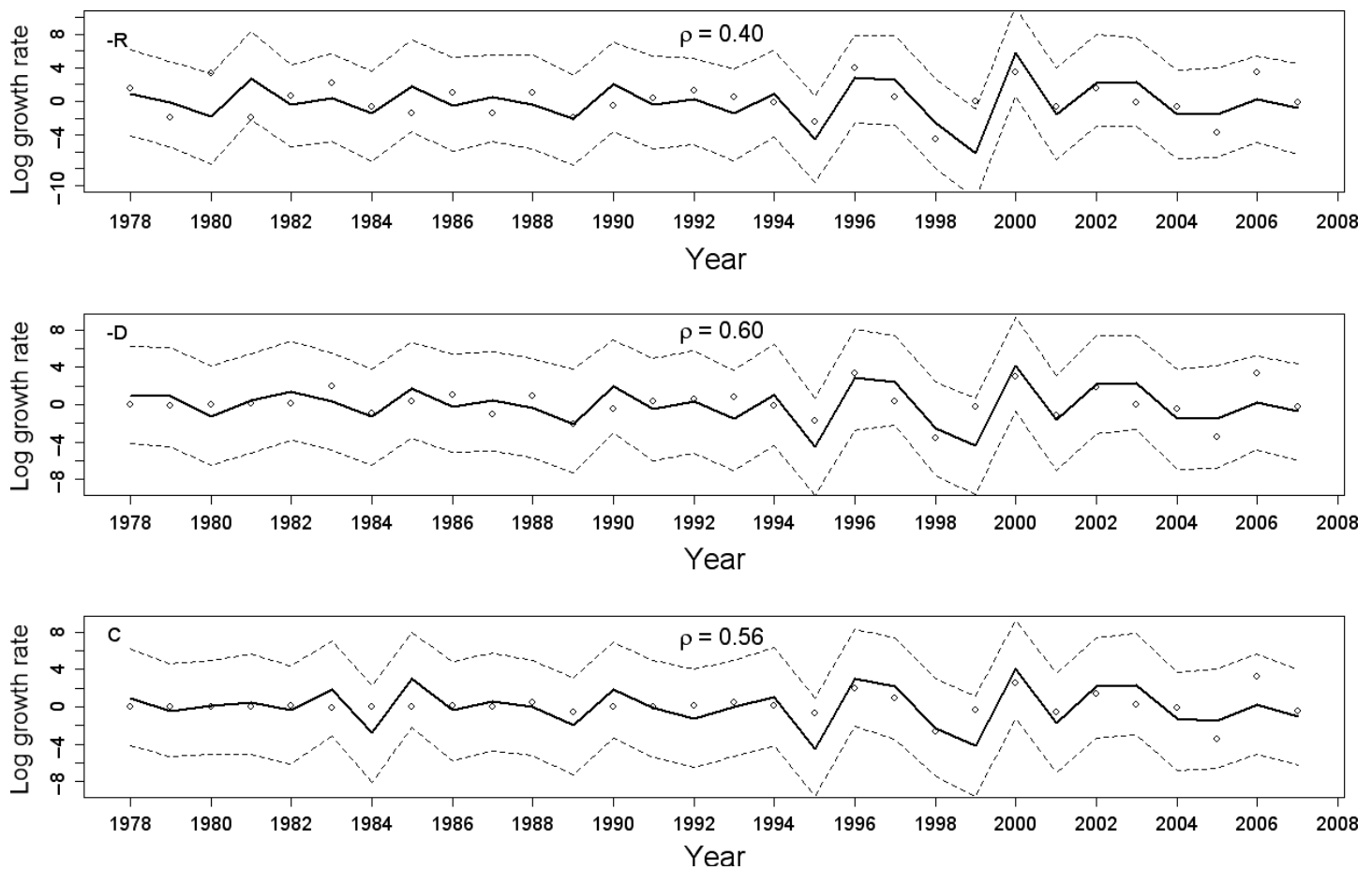
**Figure 4** The mean predicted log population growth rates of *E. cicutarium* per quadrat ($z_{j,t+1} - z_{j,t}$) given the best GLMM on rodent removal (−R), *Dipodomys* removal (−D) and control (C) plots over time (solid line) relative to observed values (open circles). Pearson correlation coefficients (ρ) denote the year relationship between predicted and observed population growth rates. Also shown are the 95% prediction envelopes (dashed lines) generated by temporal stochasticity ($\sigma^2_{year} = 3.64$).

*E. cicutarium* on control plots. The invader increased initially on rodent removal plots, while it remained relatively scarce on controls; this suggests that rodent granivory played an important role in suppressing the abundance of *E. cicutarium* at the site (Fig. 1). Furthermore, studies have shown that one of the dominant species of kangaroo rat in our community (*D. merriami*) not only consumes *E. cicutarium* seeds but prefers them over native seeds and is capable of suppressing *E. cicutarium* populations (Soholt 1973). Together, this suggests that seed predation by *Dipodomys* was indeed an important regulator of *E. cicutarium* dynamics and that the decrease of this group in the mid-1990s played an important role in the sudden increase in *E. cicutarium* on control plots.

Yet, our results also indicate that seed predation pressures were only part of the scenario leading to the sudden increase in the invasive species on control plots in the 1990s. The nonlinear relationship between *Erodium cicutarium* and precipitation (Fig. 3a) suggests that increases in *E. cicutarium* abundance also depended on a suitable climate window that co-occurred with the decline in *Dipodomys* spp. and favourable stochastic events (Figs. 3a and 4). The coincidence of the decrease in consumption followed by the precise precipitation conditions (not too wet, not too dry) created an ideal niche opportunity for *E. cicutarium* to escape control.

The relationship between *E. cicutarium* and the community of native annual forbs is less straightforward. The final global model indicates no significant relationship between the abundances of *E. cicutarium* and native annuals. However, the estimated coefficient was negative (−0.004), indicative of interspecific competition. Given the previously noted experimental evidence of the competitive suppression of natives by *E. cicutarium* at the quadrat level (Schutzenhofer & Valone 2006), as well as the trends in abundance and richness values outlined in Fig. 5, we interpret the negative coefficient as the ability of *E. cicutarium* to limit native species as opposed to the impact of competitive suppression by natives on *E. cicutarium*. Regardless of the interpretation of the non-significant but negative coefficient for interspecific competition, the strong and significant relationships of *E. cicutarium* abundance with both the resource base (precipitation) and consumer populations (rodents) indicate that changes in these aspects of the ecosystem were related to increases in the invasive *E. cicutarium*.

Populations fluctuate naturally (Bjørnstad 2001), particularly in arid systems (Brown & Heske 1990; Guo *et al.* 2002; Thibault *et al.* 2004). We do not know what exactly led to the strong decline in rodents at the site from 1990 to 1995. One possibility is climate: in the early 1990s, there were several years of low winter precipitation which resulted in few winter annual plants at the site (Fig. 1d) (Brown *et al.* 2001). We suspect that this sustained reduction in resource base likely contributed to the reduction in the rodent population, which then resulted in decreased seed predation pressure −
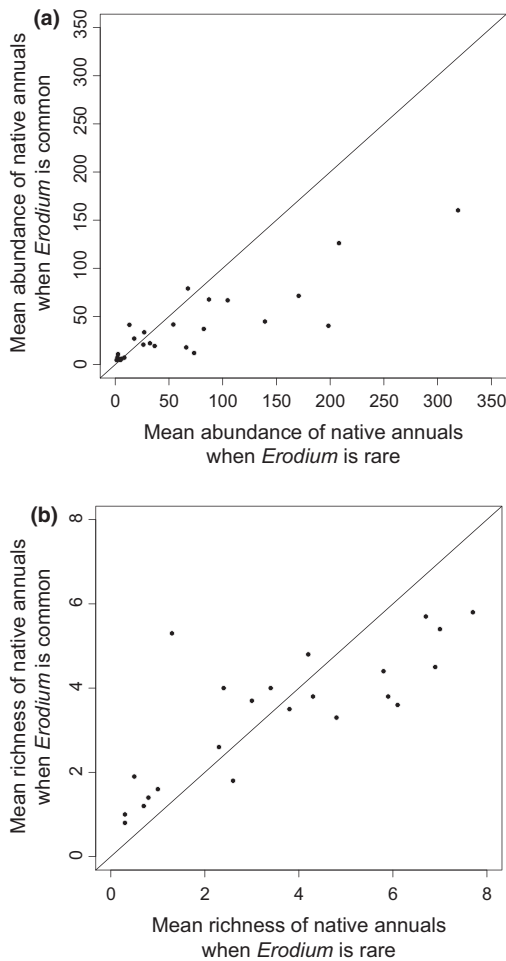
**Figure 5** Mean abundance (a) and richness (b) of native species on quadrats where *E. cicutarium* is rare (< 1% of individuals) or common (> 10% of individuals). Each point represents 1 year, where the x-coordinate is the mean abundance/richness of natives on quadrats in which *Erodium* was rare, and the y-coordinate is the mean abundance/richness of natives on quadrats in which *Erodium* was common. More points above the 1 : 1 line would indicate that natives were more abundant/exhibited greater richness when *E. cicutarium* was common, while more points below the line would indicate that natives were more abundant/exhibited greater richness when *E. cicutarium* was rare. See Fig. 2 for proportion of quadrats in each category in each year.

particularly on the large seeds. These natural fluctuations in consumer populations can result in the accumulation of the propagules that they consume, and spikes in propagule pressure can allow exotic prey to overcome biotic resistance and establish in a community (Holle & Simberloff 2005; Lockwood *et al.* 2005). Desert annual plants, including *E. cicutarium*, have a generally long-lived seed bank and the potential for delayed germination of the seed in a given year (Venable 2007). We hypothesise that the decline in rodent granivory in the early 1990s likely facilitated an accumulation of *E. cicutarium* in the seed bank. Subsequently, with favourable climate conditions, as occurred at our site in 1997 and 1998, the invader was poised to experience rapid population growth ($a = 1.49$, Fig. 4). The momentum of *E. cicutarium* population growth was sufficient to withstand the brief rebound in *Dipodomys* energy use in the late 1990s (Fig. 1b).

While past research and theory has focused on the role of overall community diversity in promoting biotic resistance (Elton 1958;

Levine & D'Antonio 1999), more recently, a variety of studies suggest that particular species are more important than overall community diversity in limiting the abundance and spread of exotics (Ruijven *et al.* 2003; Mitchell *et al.* 2006; Thomsen *et al.* 2006). In particular, natives that interact strongly with the introduced species are thought to be primarily responsible for their control (Case 1990). Our model indicates that kangaroo rats were a particularly important guild in controlling the abundance of the invader. In fact, *Dipodomys* energy requirement (DipoE) had better explanatory power than total rodent energy (AllE). Kangaroo rats dominated the rodent community for the first 20 years of the study, but declined in abundance and dominance over time (Valone *et al.* 1995; White *et al.* 2004). This decline led to a strong, temporary reduction in granivory that apparently created a niche opportunity for the invader.

Most studies of biotic resistance to invasion are short-term (Table S1), and likely fail to capture the full range of dynamics inherent in ecological systems, particularly fluctuations in consumer populations and climate conditions. Our data suggest that stochastic events on top of these variations can create potentially unpredictable niche opportunities for invaders (Fig. 4). Even in systems with strong biotic resistance, consumers may not be able to prevent exotic species from attaining high density over the long term. This phenomenon has important ramifications. First, our study demonstrates that rare exotic species can attain high abundance in a relatively short period of time if species that regulate their abundance experience a strong population decline, that is, if a 'niche opportunity' becomes available. Second, systems that currently exhibit strong biotic resistance (e.g. Table S1) may not do so in the future, particularly if control is being exerted by a few strongly interacting species. Thus, management of ecological systems to minimise the spread and dominance of exotic invaders might more profitably focus on maintaining key species interactions, rather than simply maintaining high diversity. Furthermore, this demonstrates the need for additional long-term studies that are able to capture the influence of fluctuations in climate and community dynamics on invasions.

Climate models predict more frequent extreme weather events in the coming decades (Easterling *et al.* 2000). The resulting increased environmental stochasticity will likely create new niche opportunities for introduced species via fluctuations in both resources (Bradley *et al.* 2010) and important consumers. The increase in *E. cicutarium* at this site was associated with negative effects on the abundance and diversity of native annual plants (Fig. 5) and resulted in a transformation of the community from one dominated by a high diversity of natives (Guo *et al.* 2002) to one dominated by a single exotic, *E. cicutarium* (Fig. 2). Exotic species currently regulated by strong biotic control today may come to dominate many communities in the future. This case study highlights the kinds of complex interactions that are difficult to predict, but that may be the root cause of the dominance of exotics in many systems. Understanding and predicting these changes require knowledge of existing interactions and monitoring of population fluctuations over the long term (Bradley *et al.* 2010).

## AUTHORSHIP

GRHA, TJV, MRS and SKME collected data. DNK, SKME, GRHA and TJV analysed data. GRHA and TJV wrote the first draft and SKME and DNK contributed to revisions.

## REFERENCES

Bjørnstad, O.N. (2001). Noisy clockwork: time series analysis of population fluctuations in animals. *Science*, 293, 638–643.

Bolker, B.M. (2008). *Ecological Models and Data in R*. Princeton, Princeton University Press, New Jersey.

Bolker, B.M., Brooks, M., Clark, C., Geange, S., Poulsen, J., Stevens, M. *et al.* (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.*, 24, 127–135.

Bradley, B.A., Blumenthal, D.M., Wilcove, D.S. & Ziska, L.H. (2010). Predicting plant invasions in an era of global change. *Trends Ecol. Evol.*, 25, 310–318.

Brock, R.E. & Kelt, D.A. (2004). Keystone effects of the endangered Stephens' kangaroo rat *(Dipodomys stephensi)*. *Biol. Conserv.*, 116, 131–139.

Brown, J. & Heske, E. (1990). Temporal changes in a Chihuahuan Desert rodent community. *Oikos*, 59, 290–302.

Brown, J.H. & Munger, J.C. (1985). Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology*, 66, 1545–1563.

Brown, J.H., Valone, T.J. & Curtin, C.G. (1997). Reorganization of an arid ecosystem in response to recent climate change. *P. Natl. Acad. Sci.*, 94, 9729–9733.

Brown, J., Whitham, T., Morgan Ernest, S. & Gehring, C. (2001). Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science*, 293, 643–650.

Buckley, Y.M., Briese, D.T. & Rees, M. (2003). Demography and management of the invasive plant species *Hypericum perforatum*. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. *J. Appl. Ecol.*, 40, 481–493.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A. *et al.* (2010). Global biodiversity: indicators of recent declines. *Science*, 328, 1164–1168.

Case, T. (1990). Invasion resistance arises in strongly interacting species-rich model competition communities. *P. Natl. Acad. Sci. USA*, 87, 9610.

Catford, J.A., Jansson, R. & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.*, 15, 22–40.

Chesson, P., Gebauer, R., Schwinning, S., Huntly, N., Wiegand, K., Ernest, S., Sher, A., Novoplansky, A. & Weltzin, J. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253.

Creel, S. & Creel, M. (2009). Density dependence and climate effects in Rocky Mountain elk: an application of regression with instrumental variables for population time series with sampling error. *J. Anim. Ecol.*, 78, 1291–1297.

Cushman, J., Lortie, C. & Christian, C. (2011). Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. *J. Ecol.*, 99, 524–531.

Davis, M., Grime, J. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.

Dennis, B., Ponciano, M.J., Lele, S.R., Taper, M.L. & Staples, D.F. (2006). Estimating density dependence, process noise, and observation error. *Ecol. Monogr.*, 76, 323–341.

Easterling, D.R., Meehl, G.A., Permesan, C., Chagnon, S.A., Karl, T.R. & Mearns, L.O. (2000). Climate extremes: observations, modeling, and impacts. *Science*, 289, 2068–2074.

Elton, C.S. (1958). *The Ecology of Invasions by Plants and Animals*. Methuen, London. 18.

Ernest, S., Brown, J. & Parmenter, R. (2000). Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos*, 88, 470–482.

Ernest, S., Valone, T. & Brown, J. (2009). Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA. *Ecology*, 90, 1708–1708.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N. *et al.* (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.*, 27, 233–249.

Franklin, A., Anderson, D., Gutierrez, R. & Burnham, K. (2000). Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecol. Monogr.*, 70, 539–590.

Guo, Q., Brown, J.H., Valone, T.J. & Ezcurra, E. (2002). Long-term dynamics of winter and summer annual communities in the Chihuahuan Desert. *J. Veg. Sci.*, 13, 575–584.

Hilbe, J. (2011). *Negative Bionmial Regression*. Cambridge University Press, Cambridge, UK.

Hill, S. & Kotanen, P. (2009). Evidence that phylogenetically novel non-indigenous plants experiene less herbivory. *Oecologia*, 161, 581–590.

Holle, B. & Simberloff, D. (2005). Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, 86, 3212–3218.

Kearney, T.H. & Peebles, R.H. (1960). *Arizona Flora*. University of California Press, Berkeley.

Levine, J. (2000). Species diversity and biological invasions: relating local process to community pattern. *Science*, 288, 852.

Levine, J. & D'Antonio, C. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, 87, 15–26.

Lockwood, J., Cassey, P. & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.*, 20, 223–228.

Mensing, S. & Byrne, R. (1998). Pre-mission invasion of *Erodium cicutarium* in California. *J. Biogeog.*, 25, 757–762.

Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N. *et al.* (2006). Biotic interactions and plant invasions. *Ecol. Lett.*, 9, 726–740.

O'Hara, R.B. & Kotze, D.J. (2010). Do not log-transform count data. *Method. Ecol. Evol.*, 1, 118–122.

Perkins, L.B., Leger, E.A. & Novak, R.S. (2011). Invasion triangle: an organizational framework for species invasion. *Ecol. Evol.*, 1, 610–625.

Rejmanek, M. & Richardson, D. (1996). What attributes make some plant species more invasive?: Advances in invasion ecology. *Ecology*, 77, 1655–1661.

Ruijven, J., De Deyn, G. & Berendse, F. (2003). Diversity reduces invasibility in experimental plant communities: the role of plant species. *Ecol. Lett.*, 6, 910–918.

Samson, D.A., Philippi, T.E. & Davidson, D.W. (1992). Granivory and competition as determinants of annual plant diversity in the Chihuahuan desert. *Oikos*, 65, 61–80.

Schiffman, P.M. (1994). Promotion of exotic weed establishment by endangered kangaroo rats (*Dipodomys ingens*) in a California grassland. *Biodivers. Conserv.*, 3, 524–537.

Schoolmaster, D. & Snyder, R. (2007). Invasibility in a spatiotemporally fluctuating environment is determined by the periodicity of fluctuations and resident turnover rates. *Proc. R. Soc. B*, 274, 1429–1435.

Schutzenhofer, M.R. & Valone, T.J. (2006). Positive and negative effects of exotic *Erodium cicutarium* on an arid system. *Biol. Conserv.*, 132, 376–381.

Schwarz, G. (1978). Estimating the dimension of a model. *Annals Stat.*, 6, 461–464.

Seabloom, E., Harpole, W., Reichman, O. & Tilman, D. (2003). Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences, 100, 13384–13389.

Shea, K. & Chesson, P. (2002). Community *Ecology* theory as a framework for biological invasions. *Trends Ecol. Evol.*, 17, 170–176.

Soholt, L.F. (1973). Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave Desert. *Ecol. Monogr.*, 43, 357–376.

Thibault, K., White, E. & Ernest, S. (2004). Temporal dynamics in the structure and composition of a desert rodent community. *Ecology*, 85, 2649–2655.

Thibault, K.M., Ernest, S.K.M., White, E.P., Brown, J.H. & Goheen, J.R. (2010). Long-term insights into the influence of precipitation on community dynamics in desert rodents. *J. Mammal.*, 91, 787–797.

Thomsen, M., D'Antonio, C., Suttle, K. & Sousa, W. (2006). Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. *Ecol. Lett.*, 9, 160–170.

Valone, T.J., Brown, J.H. & Jacobi, C.L. (1995). Catastrophic decline of a keystone desert rodent, *Dipodomys spectabilis*: insights from a long-term study. *J. Mammal.*, 76, 428–436.

Venable, D.L. (2007). Bet hedging in a guild of desert annuals. *Ecology*, 88, 1086–1090.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L. & Westbrooks, R. (1996). Biol. Invasions as global environmental change. Am. Sci., 84, 468–478.

White, E.P., Ernest, S.K.M. & Thibault, K.M. (2004). Trade-offs in community properties through time in a desert rodent community. *Am. Nat.*, 164, 670–676.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M. & Walker, N.J. (2009). *Zero-truncated and Zero-inflated Models for Count Data. In Mixed Effects Models and Extensions in Ecology with R.* Springer, New York, pp. 261–293.

## SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).