

## RESEARCH ARTICLE

# An experimental investigation of top-down effects of consumer diversity on producer temporal stability

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**Abstract**

1. In multitrophic systems, the diversity of consumers can affect the abundances and temporal stability of the species they consume via 'top-down' effects. However, little is known about how variation in consumer functional diversity affects the temporal stability of aggregate producer communities.
2. We use data from a long-term experiment to determine how variation in rodent granivore functional richness affected the temporal stability of the annual plant communities whose seeds they consume. Experimental plots excluded either all granivorous rodents, just large-bodied kangaroo rat granivores, or no rodents.
3. Over the 11-year period studied, reductions in rodent granivory resulted in higher annual plant community abundance and higher abundance of exotic *Erodium cicutarium*, but lower annual plant species richness and diversity. However, there was no effect of the consumer experimental treatments on annual plant community temporal stability.
4. *Synthesis.* The loss of consumers from an ecosystem need not necessarily destabilize the producer community, even when loss of consumers results in reduced producer richness and diversity.

**KEYWORDS**

annual plants, granivory, mass ratio hypothesis, multitrophic interactions, rodents, seeds, species richness

## 1 | INTRODUCTION

Ecological communities world-wide are changing, in large part due to human activities that degrade the quality of habitats, alter climate regimes, and introduce novel species (Lepczyk et al., 2008; Seabloom et al., 2006). Such changes often result in reduced community diversity and so have prompted more than two decades of research to understand how changes in diversity impact ecosystem function (Brose, & Hillebrand, 2016). One aspect of ecosystem function involves temporal stability: fluctuations in community abundance or biomass over time. Given that human activities are altering the structure and diversity of assemblages, understanding how changes in communities will affect temporal stability has become an important focus in ecology because variation in community

abundance over time can affect the level of ecosystem services provided (de Mazancourt et al., 2013; Hooper et al., 2012; Tilman, Isbell, & Cowles, 2014).

Ecologists have long recognized that communities vary in their temporal stability (Elton, 1958). Two general mechanisms to explain this variation across communities dominate theoretical work. First, community fluctuations can be stabilized by increases in community richness and diversity through compensatory dynamics and complementary resource use (the "diversity" hypothesis) (de Mazancourt et al., 2013; Tilman, Lehman, & Thomson, 1997). Second, the temporal stability of a community can be strongly influenced by the particular species it contains. For instance, the mass ratio hypothesis states that community temporal stability will be associated with the temporal stability of dominant species rather than diversity (Grime,

1998). Empirical work to date has found support for both mechanisms (Sasaki & Lauenroth, 2011; Tilman et al., 2014; Winfree, Fox, Williams, Reilly, & Cariveau, 2015) but such work has typically been restricted to the study of a single trophic level, often using synthetically constructed assemblages (Brose, & Hillebrand, 2016).

To better understand the temporal stability of natural communities, increasing attention has turned to elucidating how diversity at one trophic level affects species at another (Duffy et al., 2007; Haddad, Crutsinger, Gross, Haarstad, & Tilman, 2011). In such multitrophic systems, the diversity of consumers can affect the temporal stability of the species they consume via “top-down” effects. Theoretical work reveals that food web connectivity, the degree of consumer specialization, and species interaction strengths all can affect how changes in diversity at one trophic level affect the temporal stability of species at another, rendering general predictions difficult (Jiang, & Pu, 2009; Loreau, & de Mazancourt, 2013; Rooney, & McCann, 2011). Despite this, a growing body of empirical work has shown evidence of top-down effects of consumer diversity on the temporal stability of individual populations (Baum, & Worm, 2009; Halpern, Borer, Seabloom, & Shurin, 2005; Valone, & Schutzenhofer, 2007), but less is known about how changes in the diversity at one trophic level affect the temporal stability of entire communities at another trophic level (Britten et al., 2014; Post, 2013).

Here, we use a long-term experiment, the Portal Project, to investigate how experimental manipulations of consumer functional diversity affect the temporal stability of annual plants, the producers of the seed resources they feed upon. In the mid-1990s, the exotic annual *Erodium cicutarium* increased dramatically in abundance at the Portal site (Allington, Koons, Ernest, Schutzenhofer, & Valone, 2013). We recently showed that this invasion was associated with a change in dominance structure of the plant community (from native to an exotic species) and a decline in its richness (Valone, & Balaban-Feld, 2018). However, the temporal stability of the annual plant communities tended to increase rather than decline following invasion, a pattern opposite one might expect if temporal stability was positively associated with community diversity. Analyses revealed that in this system, annual plant community temporal stability was significantly associated with the stability of dominant species in the community rather than richness, and dominant species, including *E. cicutarium* exhibited high-temporal stability (Valone, & Balaban-Feld, 2018).

The above analyses only used data from plots that did not manipulate the rodent community. Here, we take advantage of the full experimental design of the Portal Project to examine potential top-down effects of rodent granivory on plant producer temporal stability. The rodent community at the site is diverse and includes two important functional groups of granivores (Fox, & Brown, 1993; Thibault, Ernest, & Brown, 2010): (a) large (>40 g body mass) bipedal kangaroo rats in the genus *Dipodomys* and (b) smaller (<35 g) quadrupedal mice, mainly in the genera *Chaetodipus*, *Perognathus*, and *Reithrodontomys*. In addition to body size and morphology, kangaroo rats and quadrupedal mice also differ in habitat use, with kangaroo rats foraging mainly in open areas between shrubs while mice

feed preferentially under the cover of shrubs (Rosenzweig, 1973). In addition, kangaroo rats are competitively dominant to mice and active year-round, while some mice, including *Chaetodipus penicillatus*, the numerically dominant rodent at the Portal site (Supp, Koons, & Ernest, 2015), are seasonally dormant in the winter (Brown, & Lieberman, 1973).

We examine data from control plots as well as plots that manipulated rodent abundance and functional richness to address a simple question: Does variation in granivorous rodent functional richness affect annual plant producer community temporal stability?

## 2 | MATERIALS AND METHODS

### 2.1 | Site description

Data come from a 20 ha Chihuahuan desert scrubland site established in 1977 near Portal, Arizona, USA. (Ernest et al., 2016). Dominant perennial vegetation includes *Acacia*, *Prosopis*, *Ephedra*, and *Flourensia* shrubs along with scattered perennial grasses (Valone, 2003).

The site comprises 24 0.25 ha plots that manipulate the types of rodent granivores they contain: six plots exclude all rodents (-R plots), eight plots exclude only *Dipodomys* spp. (-D plots), and 10 control plots exclude no rodents (C plots) (Ernest et al., 2016). Rodents have been continuously censused on all plots each month since 1977 and census data indicate that treatment plots differ significantly in their rodent assemblages: -R plots contain no rodents; -D plots effectively exclude kangaroo rats and so only contain small-bodied quadrupedal mice; on C plots, kangaroo rats account for over 40% of individuals captured and so both functional groups are roughly equally represented (Thibault et al., 2010). Since 1998, there have been no differences in the abundance and diversity of quadrupedal mice on C and -D plots and so the main difference between them is the presence or absence of the large-bodied kangaroo rat functional group (Thibault et al., 2010). As such, C plots have experienced higher levels of rodent granivory than -D plots because only C plots have contained both kangaroo rats and quadrupedal mice. As such, seeds on C plots have experienced granivory from both functional groups of rodents, while seeds on -D plots have only been consumed by quadrupedal mice.

Winter annual plant communities in southwestern North America germinate in response to seasonal precipitation that typically falls between December and March. Since 1989, we have counted the abundance of all annual plants rooted within 16 0.25 m<sup>2</sup> fixed sampling locations within each plot. The sampling locations were established in 1977 and include both open areas and areas under the canopy of shrubs. Annual plant censuses occur in late March or early April each year, at the end of the growing season when most species are either flowering or setting seed. Over 35 species of winter annual plants have been recorded at the site, although the number observed each year ranges widely because the abundance and diversity of these communities vary with the timing and amount of winter

precipitation (Guo, & Brown, 1996). Seed size of the annual species ranges from 0.002 to over 7.0 mg (Chen, & Valone, 2017).

Exotic annual *E. cicutarium* increased in abundance at the Portal site in the mid-1990s (Allington et al., 2013). By 1998, over 60% of the individual winter annual plants counted on plots were *E. cicutarium* and this large-seeded exotic (seed mass: 0.99 mg) dominated the site each year thereafter, representing from 38% to 88% of the community. Due to this change in the structure of the annual plant community, and to provide comparable results to Valone and Balaban-Feld (2018), we restrict data analysis to the same 11-year period examined in that study, 1998–2008, years in which *E. cicutarium* exhibited high dominance.

## 2.2 | Experimental data

For each plot each year, we calculated annual plant species richness, Shannon diversity, *E. cicutarium* abundance, total annual community abundance, and Simpson's concentration index  $\lambda$  (Simpson, 1949) (using the relative abundances of all species where  $\lambda = \sum P_i^2$  and  $P_i$  equals the relative abundance of species  $i$  [calculated as the abundance of species  $i$  on a plot and divided by total plant abundance on the plot]). The species with the largest  $P_i$  was identified as the numerically dominant species on each plot. Yearly plot values for these parameters were obtained by combining the data from the 16 sampling locations on a plot. Thus, for each year examined, we obtained a single value per plot for the above parameters.

We calculated temporal stability of the annual plant community by using the time series of yearly data on the community abundance for each plot. Community temporal stability for such a time series was calculated as the inverse of the coefficient of variation in community abundance ( $CV^{-1}$ ) which equates to  $(\mu/\sigma)$ , where  $\mu$  is the mean abundance of the community and  $\sigma$  is the standard deviation over the time period of interest (Lehman, & Tilman, 2000; Tilman, 1999) and yields a single value per plot over the time series.

## 2.3 | Statistical analyses

We used a mixed model ANOVA with repeated measures (IBM SPSS 25) to test for rodent treatment effects on plot annual plant richness, Shannon diversity, *E. cicutarium* abundance, community abundance, and Simpson's concentration index ( $\lambda$ ) ( $N = 10, 8,$  and  $6$  for C, -D, and -R treatments respectively). In these analyses, we excluded 2 years (2000, 2006) in which total abundance was 0 on all plots (i.e., very dry years with no germination of annuals at the site), resulting in 9 years of data. The repeated measures ANOVA partitions out temporal (year) effects as well as year-by-treatment interaction effects that reflect yearly changes in the annual plant community driven by variation in seasonal precipitation.

We used a one-way ANOVA to examine treatment effects on community temporal stability and the stability of the most dominant species using all 11 years of data.

## 3 | RESULTS

In the time period studied, the plant community averaged about 10 species and 600 individuals per plot per year. *E. cicutarium* dominated all 24 plots, representing about 60% of the individuals counted each year (mean *E. cicutarium*  $P_i$  was 0.55 on control plots and 0.63 on both *Dipodomys* and rodent removal plots).

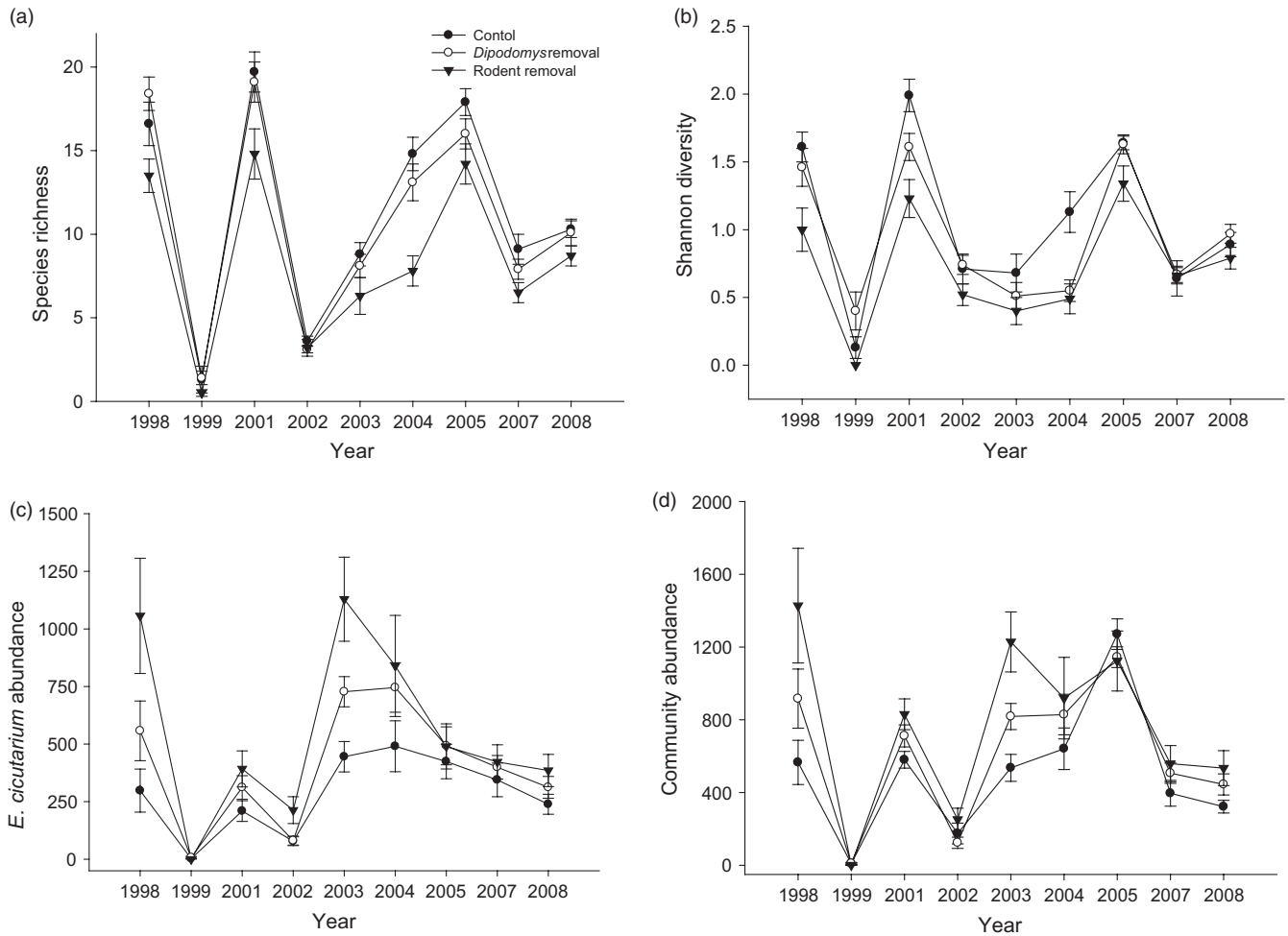
Similar to most annual plant systems, there was much year-to-year variation in the plant communities (Figure 1), but four parameters differed significantly across the rodent removal treatments (Table 1). Both annual plant species richness and Shannon diversity were highest on control plots and lowest on rodent removal plots (Figure 2a,b) (Species richness Tukey HSD post hoc tests: -R vs. -D,  $p = 0.006$ ; -R vs. C,  $p = 0.001$ ; Shannon diversity Tukey HSD post hoc tests: -R vs. -D,  $p = 0.048$ ; -R vs. C,  $p = 0.003$ ). In contrast, both *E. cicutarium* and total annual plant community abundance were highest on rodent removal plots and lowest on control plots (Figure 2c,d) (*E. cicutarium* abundance Tukey HSD test: -R vs. C,  $p = 0.021$ ; Total abundance Tukey HSD test: -R vs. C,  $p = 0.017$ ). For all four parameters, the values on *Dipodomys* removal plots were intermediate and not statistically different from values on control and all rodent removal plots (Figure 2).

In contrast, Simpson's concentration index ( $\lambda$ ) did not differ significantly across treatments (Table 1) (Mean [SE] ( $\lambda$ ): C = 0.54 [0.03]; -D = 0.52 [0.03]; -R = 0.60 [0.04]). Similarly, total annual plant community temporal stability did not differ significantly across the treatments (total abundance  $CV^{-1}$ :  $F_{2,21} = 1.3$ ,  $p = 0.30$ ) (Figure 3).

Finally, year-to-year variation in the plant community resulted in significant effects of year as well as significant year-by-treatment interactions for all parameters (Table 1; Figure 1).

## 4 | DISCUSSION

Previously, we had shown that invasion by a dominant exotic, *E. cicutarium*, was associated with a decline in annual plant community abundance and richness at this site (Valone, & Balaban-Feld, 2018). Here, we took advantage of experimental manipulations of the rodent community at the Portal site to examine how variation in the kinds of rodent granivores on plots affected the temporal stability of the plants they consume. Experimental reduction in rodent granivory resulted in increased annual plant abundance but lower richness and diversity compared to control plots, with differences being highest on plots that removed all rodents. Such top-down effects were likely driven by differences in overall levels of granivory on treatment plots, with the highest level of granivory on C plots (because kangaroo rats were only present on C plots), followed in order by -D, and then -R plots because quadrupedal mice abundance and diversity were similar on -D and C plots during the years studied (Thibault et al., 2010). Experimental reduction in rodent granivory likely enhanced annual plant seed survival explaining the higher abundance of total plants on *Dipodomys* and all rodent removal plots (Supp, Xiao, Ernest, & White, 2012). The



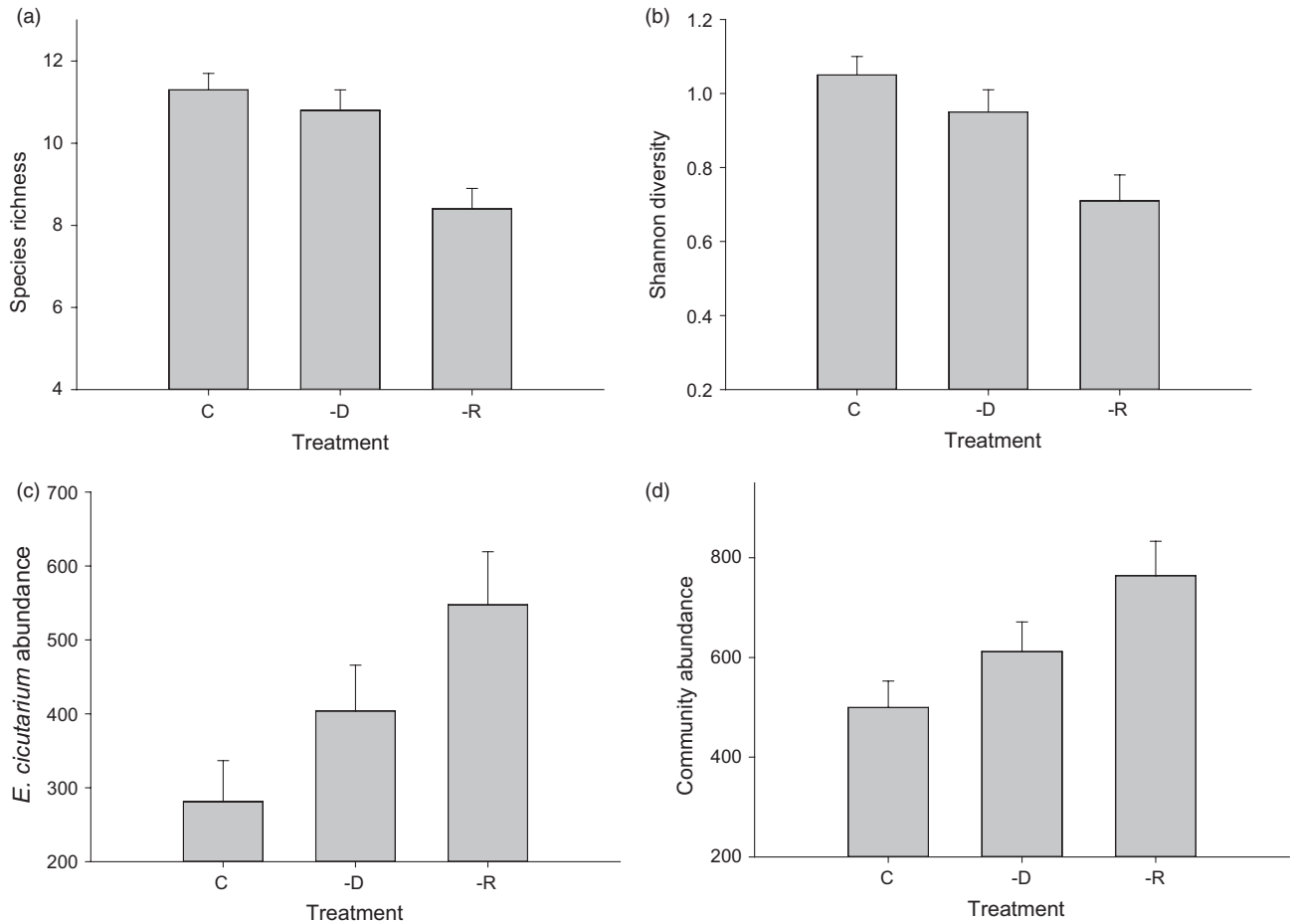
**FIGURE 1** Yearly variation in the annual plant community for the three experimental treatments. Mean (a) species richness, (b) Shannon diversity, (c) *Erodium cicutarium* abundance, and (d) total abundance. Error bars represent 95% confidence intervals

**TABLE 1** Analysis of variance results for the effect of rodent treatment and year on aspects of the plant community

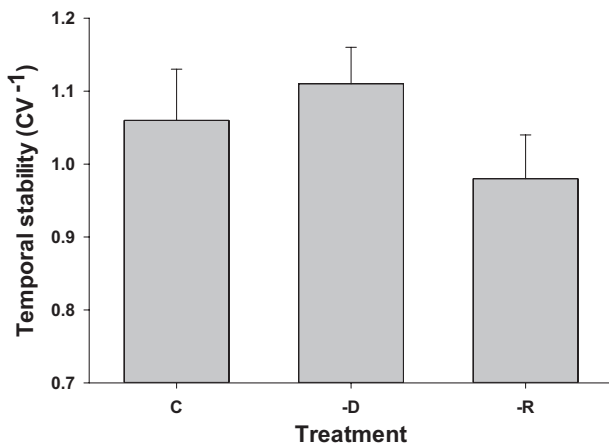
	df	Richness		Shannon diversity		<i>Erodium cicutarium</i> abundance		Total abundance		Simpson's concentration index $\lambda$	
		F	p	F	p	F	p	F	p	F	p
Between subjects											
Treatment (T)	2	10.6	0.001	7.1	0.004	4.3	0.03	4.6	0.022	1.4	0.26
Error	21										
Within subjects											
Year (Y)	8	154.1	0.001	76.3	0.001	45.2	0.001	57.8	0.001	19.8	0.001
Y × T	16	2.1	0.01	3.1	0.001	4.4	0.001	3.6	0.001	3.6	0.001
Error	168										

increase in large-seeded *E. cicutarium* abundance on such plots can also explain the concomitant decrease in annual plant richness and diversity because this exotic is known to competitively suppress natives: experimental removal of *E. cicutarium* is known to result in higher abundance and diversity of native annuals (Ignace, & Chesson, 2014; Schutzenhofer & Valone, 2006).

An important finding of our work is that experimental manipulation of rodent consumer functional diversity did not have a significant effect on the temporal stability of the annual plant communities, despite the above-mentioned significant effects on annual plant richness and diversity. Why? We offer three explanations for the lack of rodent consumer treatment effects on plant producer



**FIGURE 2** Treatment effects on the plant community. Mean (a) species richness, (b) Shannon diversity, (c) *Erodium cicutarium* abundance, and (d) total abundance. Error bars represent 95% confidence intervals. Both bipedal kangaroo rats and quadrupedal mice were present on control plots (C). Only mice were present on *Dipodomys* removal plots (-D), while no rodents were present on rodent removal plots (-R)



**FIGURE 3** Treatment effects on annual plant community temporal stability (CV<sup>-1</sup>). Both bipedal kangaroo rats and quadrupedal mice were present on control plots (C). Only mice were present on *Dipodomys* removal plots (-D), while no rodents were present on rodent removal plots (-R)

temporal stability. First rodent granivores in southwestern North America are opportunistic consumers of seeds, primarily those of winter annual plants (Davidson, Samson, & Inouye, 1985). As such,

they have broad dietary overlap and appear to partition resources mainly by microhabitat (by foraging under shrubs or in the open) rather than by consuming different species of seeds (Stamp, & Ohmart, 1978, cf. Ernest, & Brown, 2001). Such a system may reduce the impact of the loss of specific species or functional groups of consumers on individual producer abundance and community temporal stability (Duffy et al., 2007; Loreau, & de Mazancourt, 2013; Rooney, & McCann, 2011).

Second, in this annual plant system, rodent consumers feed on plant seeds rather than directly on adult plants, and so variation in consumer pressure on adult annual plant abundance is mediated through effects on the seed bank (e.g., Brown, & Heske, 1990; Howe, & Brown, 2000). This makes our system different from other work that has examined top-down effects of rodent consumers on plant communities (e.g., Howe, Zorn-Arnold, Sullivan, & Brown, 2006). While prior work has revealed how rodent granivory and yearly precipitation influence annual plant abundances in this system (Chen, & Valone, 2017; Ernest, Brown, & Parmenter, 2000; Guo, & Brown, 1996; Heske, Brown, & Guo, 1993), and our data show consistent effects of the rodent consumer treatments on several important aspects of the plant community, we found no significant

effect on annual plant community temporal stability, perhaps because of unknown mechanisms that link seed bank granivory and yearly precipitation to plant emergence, and influence temporal stability (Allington et al., 2013). Additional work is required to further explore this possibility.

Third, recent work on natural systems often finds weak or no relationships between temporal stability and community richness and diversity (Mortensen et al., 2018; Valone, & Balaban-Feld, 2018; Wardle, 2016; Yang et al., 2017). Natural communities typically exhibit high dominance, a factor known to reduce the stabilizing effect of diversity (Doak et al., 1998). Not surprisingly, our system exhibited high dominance with *E. cicutarium* representing over 50% of the individuals recorded each year, on average. Consumers can often limit the abundance of dominant species, which then can promote higher producer diversity by reducing competitive suppression of subordinate species (Hautier, Niklaus, & Hector, 2009). When temporal stability is positively associated with diversity, reductions in consumers can result in increased dominance and reduced producer richness and a reduction in temporal stability (Mortensen et al., 2018). In the Portal system, however, we have observed much stronger relationships between community temporal stability and the stability of the most dominant species (*E. cicutarium*) (Valone, & Balaban-Feld, 2018), a pattern often found in studies of natural communities (Hillebrand, Bennett, & Cadotte, 2008; Sasaki & Lauenroth, 2011; Winfree et al., 2015). While the rodent consumer treatments affected *E. cicutarium* abundance, they did not fundamentally change the dominance structure ( $\lambda$ ) of the plant communities across the treatments (Table 1). Thus, while variation in consumer diversity affected plant community richness and diversity, these effects did not translate into effects on annual plant community dominance structure and producer community temporal stability. Other multitrophic studies of the effects of trophic diversity on community (rather than population) temporal stability have found idiosyncratic results (Baum, & Worm, 2009; Britten et al., 2014; Bruno, & Cardinale, 2008; Eisenhauer et al., 2011; Mortensen et al., 2018; Post, 2013; Ramus, & Long, 2016) strongly suggesting that factors other than diversity may often affect community temporal stability, as we observed.

Examination of diversity effects on ecosystem function, including temporal stability, has often relied on manipulation of community richness using synthetically constructed communities on sown plots (Tilman, Reich, & Knops, 2006). Our use of experimental plots, in a natural system that manipulated rodent functional richness, provides an alternative approach to studying how variation in diversity at one trophic level can affect temporal stability at another. To further understand how variation in rodent functional diversity affects annual plant communities, one would like to examine plots that remove only quadrupedal mice, but such treatment plots are lacking due to logistical issues involved in creating and maintaining such a treatment. Despite this shortcoming, our work, in some ways, mimics the kinds of consumer species losses occurring world-wide that tend to be biased towards species of large body size (Cardillo et al., 2005), and so may provide important insight into effects occurring in many natural communities. Additional work from both synthetic and

natural communities will provide greater understanding of how multitrophic communities will respond to the ongoing loss of species.

#### 4.1 | Implications

In many ecosystems, anthropogenic activities frequently result in reduced biodiversity across multiple trophic levels (Hooper et al., 2012; Naeem, Duffy, & Zavaleta, 2012). Our results suggest that reductions in consumer diversity may result in reduced diversity of producers but have little effect on producer temporal stability (Mortensen et al., 2018). Our work highlights the need for continued experimental investigation of the effects of consumer diversity and dominant species on producer temporal stability in multitrophic systems.

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#### AUTHOR'S CONTRIBUTIONS

T.J.V. developed and framed the research questions; T.J.V. and J.B.-F. analysed the data; T.J.V. led the writing of the manuscript. T.J.V. and J.B.-F. contributed to drafts and gave approval for publication.

#### DATA ACCESSIBILITY

Data available at <https://doi.org/10.5281/zenodo.1215988> (Ernest et al., 2018).

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