



SPECIAL FEATURE: DYNAMIC DESERTS

Shrub encroachment, productivity pulses, and core-transient dynamics of Chihuahuan Desert rodents

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Abstract. Drylands worldwide are experiencing shrub encroachment into grasslands with potential consequences for biodiversity and ecosystem services. Climate change could increase the rate of shrub encroachment, amplify precipitation variability, and thus alter bottom-up processes for animal communities. Desert rodents are important biodiversity elements of arid grasslands and shrublands that exert strong effects on soil, vegetation, and other animal species. We used long-term data from the Jornada Basin Long Term Ecological Research site in the Chihuahuan Desert of southern New Mexico to ask whether bottom-up control of desert rodents changes across shrub encroachment gradients. Our design included spatial blocks with replicated ecological states representing transitions from black grama (*Bouteloua eriopoda*) to honey mesquite (*Prosopis glandulosa*). Grassland-to-shrubland transitions did not produce degraded ecosystems, on average, with reduced net primary production or decreased rodent biomass. However, more rodent biomass was supported on unencroached grasslands following droughts whose frequency and severity may increase in southwestern United States. Hence, the observed evenness in rodent biomass across ecological states should be sensitive to climate change. The best predictors of rodent biomass also differed markedly for two trophic groups. This outcome was explained by considering core-transient dynamics. Granivores were mostly core species that regularly occurred on sites and responded to lagged net primary production at local scales, whereas folivores included transient species (especially *Sigmodon hispidus*) that responded to lagged precipitation at broader scales via spillover dynamics. Bottom-up processes for desert rodents across shrub invasion gradients were understood by integrating lagged responses to productivity pulses with core-transient structuring of communities.

Key words: bottom-up control; Chihuahuan Desert; net primary production; precipitation variability; *Prosopis glandulosa*; rodent communities; shrub encroachment; Special Feature: Dynamic Deserts.

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INTRODUCTION

Drylands cover 41% of the earth (MEA 2005) and are experiencing shrub encroachment into grasslands (Naito and Cairns 2011, Archer and

Predick 2014) with potential consequences for biodiversity and ecosystem services (Eldridge et al. 2011, Stanton et al. 2017). In the Chihuahuan Desert of southwestern United States, encroachment of grasslands by honey mesquite

(*Prosopis glandulosa*) and creosotebush (*Larrea tridentata*) has been pervasive (Peters et al. 2012, 2015). Multiple factors have triggered and reinforced these state transitions including severe drought, overgrazing by livestock, reduced fire frequencies, CO₂ enrichment, and spatial contagion (Okin et al. 2015, Peters et al. 2015; Bestelmeyer et al., *in press*). Grassland-to-shrubland transitions are viewed as a form of land degradation (i.e., desertification; MEA 2005, Bestelmeyer et al. 2015) that does not reverse easily without intervention (Bestelmeyer et al. 2015). This hysteresis has prompted large-scale shrub control programs by management agencies (Coffman et al. 2014, Cosentino et al. 2014; Bestelmeyer et al., *in press*). However, equating shrub encroachment to degradation is not universally supported (Eldridge et al. 2011). Responses of vertebrates to shrub encroachment can be negative, neutral, or positive (Whitford 1997, Eldridge et al. 2011, Coffman et al. 2014, Stanton et al. 2017). Negative effects on vertebrate diversity are more common for mammals and herpetofauna and for regions with low net primary productivity (Stanton et al. 2017).

Primary and secondary consumers in drylands can be controlled by precipitation events that trigger productivity pulses (Reynolds et al. 2004) that cause strong population fluctuations over time via direct and indirect mechanisms (Báez et al. 2006, Holmgren et al. 2006, Meserve et al. 2011, Deguines et al. 2017). Desert rodents can irrupt following productivity pulses and then greatly affect vegetation and ecosystem processes via selective herbivory, biopedturbation, and ecosystem engineering (Brown and Heske 1990, Whitford and Bestelmeyer 2006, Kelt 2011). Generalizations about bottom-up regulation of desert rodents, and how it changes with shrub encroachment, have been difficult to establish (Brown and Ernest 2002, Thibault et al. 2010, Lightfoot et al. 2012). This difficulty may have its roots in the lack of long-term datasets that are arrayed across grassland and shrubland states, but that experience similar precipitation regimes. Furthermore, many existing studies have only measured precipitation and have not directly measured aboveground net primary production (ANPP), a key link in the bottom-up chain, and or have relied on proxies for plant productivity (Thibault et al. 2010, Hernández et al. 2011).

Moreover, spatial dynamics and metacommunity processes have only recently become a focus for desert rodents (Stevens and Tello 2012), and their role in bottom-up regulation could be underestimated. Specifically, an understanding of how core-transient dynamics at landscape scales (Supp et al. 2015) respond to precipitation variability is necessary to explain population fluctuations at site scales. Core species are persistent species that normally occur on sites, whereas transient species only infrequently appear, and their dynamics are driven by broader landscape heterogeneity (Magurran and Henderson 2003, Coyle et al. 2013). The spatial pattern of primary production across landscapes may govern dynamics of transient species (Fernández et al. 2016), which could affect local fluctuations of rodent biomass independently of local changes in primary production.

Climate change models predict that prolonged droughts punctuated by extreme precipitation events will become more frequent for the southwestern United States (Cook et al. 2015, Prein et al. 2016). Such changes could greatly alter the nature of bottom-up trophic cascades. Moreover, increased precipitation variability could favor shrubs over grasses due to their contrasting root distributions and asymmetric responses to wet and dry periods (Gherardi and Sala 2015). Hence, climate change could not only alter rainfall input into the Chihuahuan Desert, but also the pace of shrub encroachment and the resulting landscape on which resource pulses are translated into consumer biomass.

Here, we use long-term data from the Jornada Basin Long Term Ecological Research (LTER) site to examine bottom-up processes for Chihuahuan Desert rodent communities across shrub invasion gradients. First, we examine the link between precipitation and net primary production across ecological states. Then, we ask whether shrub encroachment produces degraded landscapes with decreased plant productivity and reduced rodent biomass. If shrubland states are associated with a loss of ANPP, particularly of plant species consumed by rodents, then rodent biomass should decline across shrub encroachment gradients. Alternatively, species composition of the community might shift in a compensatory manner toward species that can exploit shrubland resources, providing stability in rodent biomass

across the gradients (Ernest et al. 2008). Next, we test the expectation that measures of plant productivity should be better predictors of rodent biomass than precipitation, and ask whether these outcomes differ among trophic groups and involve time lags. Finally, we place our results in the context of core-transient dynamics to explain observed community responses of desert rodents to precipitation pulses across ecological states.

LANDSCAPE SETTING AND STUDY DESIGN

The study was conducted at the Jornada Basin LTER site in southern New Mexico, USA (32°35' N, 106°51' W; 1334 m a.s.l.). This expansive 100,000-ha site includes the Jornada Experimental Range and the Chihuahuan Desert Rangeland Research Center. All of our study sites were edaphically similar with sandy to sandy loam surface soils and typically a petrocalcic horizon at depths of 30–100 cm. Changes over time in ecological states at Jornada Basin have been extreme. In 1858, 67% of the area was dominated by upland grasslands that included black grama (*Bouteloua eriopoda*). By 1998, these grasslands had been reduced to 3% (Peters et al. 2012). During this same period, there was extensive encroachment of honey mesquite with areas dominated by mesquite increasing from 15% to 59% (Peters et al. 2012). Cattle grazing occurs throughout Jornada Basin but conservative stocking rates are now maintained (Havstad et al. 2006). The long-term mean annual precipitation is 245 mm with much coming from monsoonal rainfall during the summer, especially from July to September (Wainwright 2006).

We sampled three spatial blocks (pastures) each containing three sites (grassland, ecotone, and shrubland states) representing a gradient in shrub encroachment (Fig. 1). Blocks were 5–13 km apart. Each site was 3 ha (100 × 300 m). Within a block, distances to the nearest other site ranged from 188 to 558 m. Variations in shrub cover defining ecotones are most likely due to gradual, spatially contagious spread of shrubs into grasslands (Bestelmeyer et al. 2011), but all grassland sites have the potential to convert to shrubland based on their soil characteristics.

We measured vegetation cover on each site via line-point intercept sampling (Herrick et al. 2005) in 2003, 2009, and 2013. Here, we provide grand

a) Grassland



b) Ecotone



c) Shrubland



Fig. 1. Examples of three ecological states where desert rodent sampling occurred at the Jornada Basin Long Term Ecological Research site. (a) Grassland state with transitional ecotone on horizon. (b) Ecotone state including mix of perennial grasses and honey mesquite (*Prosopis glandulosa*). (c) Shrubland state dominated by mesquite. Our mesquite shrublands had not progressed to forming dunes.

means across the three replicate sites and 3 yr ($n = 9$) for descriptive purposes (see Appendix S1: Fig. S1 for additional details). Grassland sites had 37.1% (standard error [SE] = 4.6%) perennial

grass cover and 3.9% (SE = 0.75%) shrub cover. Ecotone sites had 30.6% (SE = 5.5%) perennial grass cover and 9.9% (SE = 0.7%) shrub cover. Shrubland sites had 16.3% (SE = 4.6%) perennial grass cover and 12.2% (SE = 0.8%) shrub cover. Coverage by bare soil was higher on shrublands (53.4%, SE = 4.2%) than on grasslands (36.6%, SE = 5.6%) and ecotones (38.4%, SE = 5.0%). Across all sites, black grama (*Bouteloua eriopoda*) was the most abundant perennial grass (mean = 68.4% of perennial grass cover, standard deviation [SD] = 20.0%, $n = 9$). Other perennial grasses included *Sporobolus* spp., *Aristida* spp., *Muhlenbergia porteri*, and *Dasyochloa pulchella*. Many forbs and annual grasses were present, and their cover was highly variable in space and time. Honey mesquite was the dominant shrub species (mean = 78.3% of shrub cover, SD = 12.9%, $n = 9$). Other shrub species included *Yucca elata*, *Ephedra trifurca*, and *Ephedra torreyana*. Common sub-shrubs included *Gutierrezia sarothrae* and *Zinnia acerosa*. In sum, we sampled desert rodents across replicated ecological states representing black grama-to-mesquite gradients.

LINKING PRECIPITATION AND PLANT PRODUCTIVITY

Water availability is the main factor limiting ANPP in arid and semiarid environments (Sala et al. 2012). Nevertheless, relationships between ANPP and precipitation can be difficult to detect (Huenneke et al. 2002) and depend on sequences of wet and dry years (Peters et al. 2012). In particular, ANPP–precipitation relationships can involve legacies in which the current-year ANPP depends not only on current-year precipitation but also on the previous-year ANPP (Sala et al. 2012). Although one might expect that shrub encroachment could reduce primary production due to loss of soil resources in bare intershrub spaces (Huenneke et al. 2002), differences in average ANPP across years between grasslands and mesquite shrublands are minor (Huenneke et al. 2002) or nonexistent (Peters et al. 2012, Williamson et al. 2012). However, the relationship between ANPP and annual precipitation can weaken with increasing shrub cover (Peters et al. 2012, Williamson et al. 2012). Hence, we predicted that net primary production would be unrelated to shrub cover on average, but ANPP

could depend on an interaction between precipitation and shrub cover.

We measured precipitation for winter (November–April) and summer (May–October). Hence, current year indicates the 12 months leading up to rodent sampling (i.e., water year instead of calendar year). Precipitation was measured with rain gauges specific to each spatial block. The distance between a site and a rain gauge varied from 53 to 2250 m but most measurements (76%) were within 824 m. Summer precipitation averaged 173.5 mm (SE = 17.2, $n = 33$), and winter precipitation averaged 55.6 mm (SE = 8.9, $n = 33$).

We measured ANPP following a volumetric method developed by Huenneke et al. (2001). Sampling occurred at the end of the growing season each spring (April) and fall (October) starting in 2005. On each site, measurements were taken on thirty-two 1-m² permanent quadrats distributed on two parallel transects (55 m apart) of 16 quadrats each (20-m spacing). We used cover and height to estimate the volume of each plant. Plant biomass was then estimated non-destructively using the regressions of live biomass vs. plant volume derived from previously gathered harvest data (Huenneke et al. 2001). For shrubs, sub-shrubs, perennial grasses and forbs, and summer annuals, the spring (pre-growth) biomass was treated as the baseline and ANPP was estimated as the difference between the fall and spring standing biomass. Conversely, for winter annual forbs the baseline was set at zero and the standing biomass during spring was treated as ANPP. For analyses, we examined total ANPP and annuals ANPP (production by annual grasses and forbs), which should be a better surrogate for abundance of seeds preferred by granivorous rodent species (Thibault et al. 2010, Lightfoot et al. 2012).

We evaluated relationships between ANPP and precipitation over years and across ecological states. Using data from 2005 to 2014, we constructed mixed models (MIXED Procedure, SAS Institute 2013) with either total ANPP or annuals ANPP as the response variable, spatial block as a fixed effect, and combinations of current-year summer precipitation, current-year winter precipitation, shrub cover, and interactions between precipitation and shrub cover as fixed effects (Appendix S2: Table S1). Year was modeled as a

repeated measure with an autoregressive (1) covariance structure, which would account for any legacy effects on ANPP (Sala et al. 2012). We evaluated models throughout this study using an information theoretic approach (Burnham and Anderson 2002). Models with a Δ Akaike's information criterion (AIC) value ≤ 2.0 were considered competitive, and we assessed model fit of competitive models when making inferences to avoid support of uninformative variables (Arnold 2010).

For total ANPP, all competitive models included current year's summer precipitation, and current year's winter precipitation was in the second-ranked model and explained some variation (Appendix S2: Table S1). Shrub cover was in the third-ranked model but did not improve model fit substantially (Appendix S2: Table S1). Hence, total ANPP was related mainly to summer precipitation ($\beta = 0.262$, $SE = 0.072$) and secondarily to winter precipitation ($\beta = 0.204$, $SE = 0.142$; Fig. 2a) from the current year. For annuals ANPP, there was only one competitive model (Appendix S2: Table S1) that included the positive effects of current year's summer precipitation ($\beta = 0.080$, $SE = 0.013$) and winter precipitation ($\beta = 0.063$, $SE = 0.026$) and the negative effect of shrub cover ($\beta = -0.741$, $SE = 0.332$; Fig. 2b). There was no support for an interaction between precipitation and shrub cover for explaining ANPP for either total production or production of annuals (Appendix S2: Table S1).

Although total ANPP was similar across ecological states, the proportion of primary production contributed by perennial shrubs, mainly mesquite, increased from 6.5% ($SE = 2.2\%$) on grasslands to 23.6% ($SE = 4.3\%$) on shrublands. Thus, the productivity from herbaceous plants, which provide most of the food resources for desert rodents in the Chihuahuan Desert (Hope and Parmenter 2007, Thibault et al. 2010, Lightfoot et al. 2012), was reduced on shrublands. Of our core species, only *Neotoma leucodon* is reported to eat mesquite seeds other than incidentally (Hope and Parmenter 2007). Likewise, the estimated production from annuals was less on shrubbier sites, possibly due to a reduction of soil resources. Hence, food resources available to rodents should decline with shrub encroachment even though total net primary production remains unchanged.

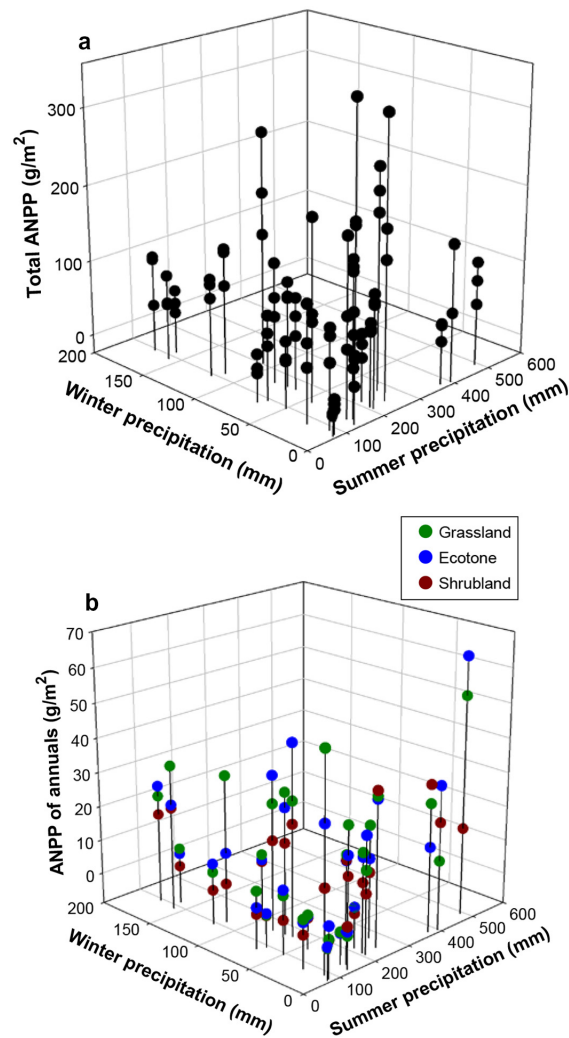


Fig. 2. Positive influence of summer and winter precipitation on (a) Total aboveground net primary production (ANPP) and (b) ANPP of annual grasses and forbs at Jornada Basin Long Term Ecological Research site, 2005–2014. ANPP of annuals was also negatively related to shrub cover.

DOES SHRUB ENCROACHMENT DEGRADE HABITAT FOR DESERT RODENTS?

Previous studies that have compared abundance or biomass of Chihuahuan Desert rodents in distinct grassland vs. shrubland habitats have focused on creosotebush-dominated shrublands (Whitford 1976, Báez et al. 2006, Lightfoot et al. 2012) or mixed shrublands (Hernández et al. 2005). These studies often included no replication

with a single grassland site and a single shrubland site that occurred on different soils that would normally support different shrub species (Whitford 1976, Hernández et al. 2005, Lightfoot et al. 2012). Our study design is unique in that it mimics mesquite encroachment by using spatial replicates of mesquite shrublands, ecotones, and grasslands all on the same sandy soils susceptible to mesquite invasion.

Based on ANPP patterns from our study, we predicted that rodent biomass, at least following resource pulses, would be highest on grasslands, intermediate on ecotones, and lowest on shrublands. This prediction derives solely from expectations regarding bottom-up processes, however, and outcomes could differ if shrub encroachment alters the strength of top-down processes (Blaum et al. 2007).

On each 3-ha site, we sampled small mammals with 96 traps (Sherman model XLKR baited with oats) in a 6 × 16 grid (20-m spacing between traps). From 2004 to 2007, livetrapping occurred mostly during July. From 2008 to 2014, when the project became part of long-term sampling by Jornada Basin LTER program, livetrapping occurred during October. We account for this difference in time of sampling when relevant in our analyses below. We trapped each site for four consecutive nights each year. Sites within a

spatial block were trapped during the same week. We marked captured individuals with uniquely numbered ear tags, or with a permanent pen on their ventral side for smaller species, and we recorded their body mass. For analyses, nocturnal rodent species were assigned to one of three trophic groups: granivores, folivores, and omnivores (Table 1).

Patterns for abundance and biomass can become decoupled if the mean body mass of species changes across space or time (White et al. 2004, Hernández et al. 2011). Hence, we compared species ranks within rodent communities for the three ecological states by plotting rank-abundance curves with biomass overlaid (Thibault et al. 2004). Next, we used linear mixed models to ask whether total rodent abundance or biomass changed with shrub encroachment, and whether such effects only occurred during certain years. We also asked whether shrub encroachment affects trophic groups differently by running linear mixed models separately for granivores, folivores, and omnivores. We focused on biomass responses for trophic groups because of our main interest in determining how primary productivity translates into rodent biomass across ecological states. The mixed models used a normal error distribution and included shrub cover and spatial block as fixed effects, year as a

Table 1. Assignment of trophic groups and core-transient status for Chihuahuan Desert rodents on three ecological states from Jornada Basin Long Term Ecological Research, New Mexico site, 2004–2014.

Trophic group	Species	Core-transient designation		
		Grassland	Ecotone	Shrubland
Granivores	<i>Chaetodipus eremicus</i>	Core (1.00)	Core (1.00)	Core (1.00)
	<i>Dipodomys merriami</i>	Core (0.82)	Core (1.00)	Core (1.00)
	<i>Dipodomys ordii</i>	Core (1.00)	Core (1.00)	Core (1.00)
	<i>Dipodomys spectabilis</i>	Core (1.00)	Core (0.91)	Core (0.73)
	<i>Perognathus flavus</i>	Core (0.91)	Core (0.91)	IT (0.46)
Folivores	<i>Neotoma leucodon</i>	Core (0.73)	Core (0.91)	Core (0.55)
	<i>Neotoma micropus</i>	IT (0.36)	Core (0.82)	Core (0.64)
	<i>Sigmodon hispidus</i>	ET (0.27)	ET (0.46)	ET (0.36)
Omnivores	<i>Onychomys arenicola</i>	ET (0.27)	ET (0.09)	ET (0.18)
	<i>Onychomys leucogaster</i>	Core (0.73)	Core (0.82)	Core (0.64)
	<i>Peromyscus eremicus</i>	ET (0.09)	ET (0.09)	ET (0.09)
	<i>Peromyscus leucopus</i>	(0.00)	ET (0.09)	(0.00)
	<i>Peromyscus maniculatus</i>	(0.00)	ET (0.09)	ET (0.09)

Notes: Core-transient designation shows in parentheses the proportion of years out of 11 that species occurred in the ecological state. Core species occurred on a state >50% of the years. Internal transients (IT) occurred on an ecological state <50% of the years but were a core species in another state. External transients occurred during <50% of the years on all states. Taxonomy follows Frey (2004). *Chaetodipus eremicus* was formerly *Chaetodipus penicillatus*. *Neotoma leucodon* was formerly *Neotoma albigula*.

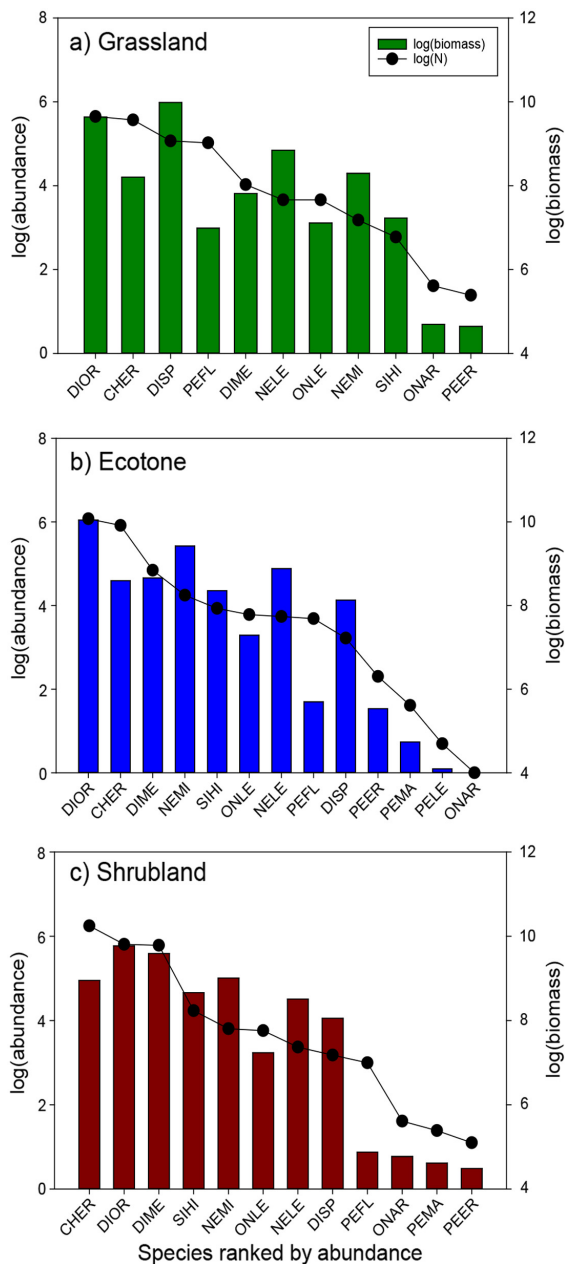


Fig. 3. Rank–abundance curves (lines) with biomass superimposed (bars) for species of Chihuahuan Desert rodents at Jornada Basin Long Term Ecological Research site. Species abundance and biomass totals are for 11 yr (2004–2014) and three replicates for each ecological state: a) grassland, b) ecotone, and c) shrubland. Codes indicate the species name: *Dipodomys ordii* (DIOR), *Dipodomys merriami* (DIME), *Dipodomys spectabilis* (DISP), *Chaetodipus eremicus* (CHER), *Perognathus flavus* (PEFL), *Neotoma leucodon* (NELE), *Neotoma*

repeated measure with an autoregressive (1) covariance structure, and a year \times shrub cover interaction (MIXED Procedure, SAS Institute 2013). Rodent abundance was log-transformed to meet model assumptions regarding normality.

Across the study, we captured 3658 individuals representing 13 species (Table 1). There were substantial shifts in the desert rodent community across ecological states (Fig. 3). For instance, *Dipodomys spectabilis* decreased greatly from grasslands to shrublands (abundance rank: 3 \rightarrow 8; biomass rank: 1 \rightarrow 7). These changes are consistent with our understanding of *D. spectabilis* as a keystone species of desert grasslands that does not tolerate high shrub cover (Krogh et al. 2002, Cosentino et al. 2014). *Sigmodon hispidus* exemplifies the opposite pattern as it increased from grasslands to shrublands (abundance rank: 9 \rightarrow 4; biomass rank: 7 \rightarrow 4). Finally, *Neotoma micropus* was most abundant on the transitioning ecotone sites where it was the second-ranked species in terms of biomass produced (Fig. 3). Our results support the general idea that community structure of Chihuahuan Desert rodents is sensitive to shrub cover (Brown et al. 1997, White et al. 2004, Hernández et al. 2005, Lightfoot et al. 2012).

Total rodent abundance and biomass varied dramatically over time with peaks in 2007, 2009, and 2014 following years with above average summer precipitation (Fig. 4). Abundance of rodents was affected by shrub cover but the direction was for greater abundances on shrubbier sites (Fig. 4a; Appendix S2: Table S2). In contrast, total rodent biomass was on average similar across ecological states (Fig. 4b; Appendix S2: Table S2). The model for biomass that included an interaction between shrub cover and year was not supported despite improving model fit because it required many parameters (Appendix S2: Table S2). Nevertheless, there was evidence that rodent biomass was lower on grasslands than on shrubbier sites in some years (2007 and 2008) but higher on grasslands during a dry period (2011 and 2012; Fig. 4b).

(Fig. 3. Continued)

micropus (NEMI), *Sigmodon hispidus* (SIHI), *Onychomys leucogaster* (ONLE), *Onychomys arenicola* (ONAR), *Peromyscus eremicus* (PEER), *Peromyscus leucopus* (PELE), *Peromyscus maniculatus* (PEMA).

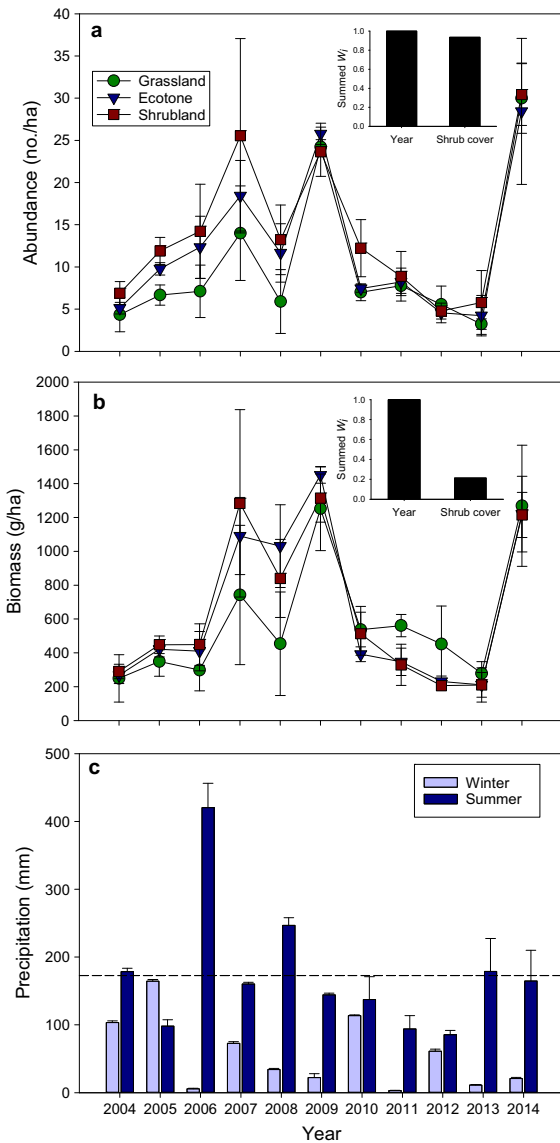


Fig. 4. (a) Total abundance and (b) total biomass of desert rodents at Jornada Basin Long Term Ecological Research (LTER) site, 2004–2014. Means (± 1 standard error [SE]) are from three spatial blocks for each ecological state. Insets indicate support for models including year or shrub cover as predictors (see Appendix S2: Table S2). (c) Annual patterns of summer and winter precipitation at Jornada Basin LTER site. Bars are means (± 1 SE) for three spatial blocks. The dotted horizontal line indicates the 11-yr mean for summer precipitation.

Partitioning biomass among trophic groups revealed that both granivores and omnivores produced similar biomass across habitats,

whereas biomass of folivores was greater on shrubbier sites (Fig. 5; Appendix S2: Table S2). Temporal dynamics also differed among the trophic groups in that granivores did not exhibit a sharp peak in 2007, whereas folivores peaked

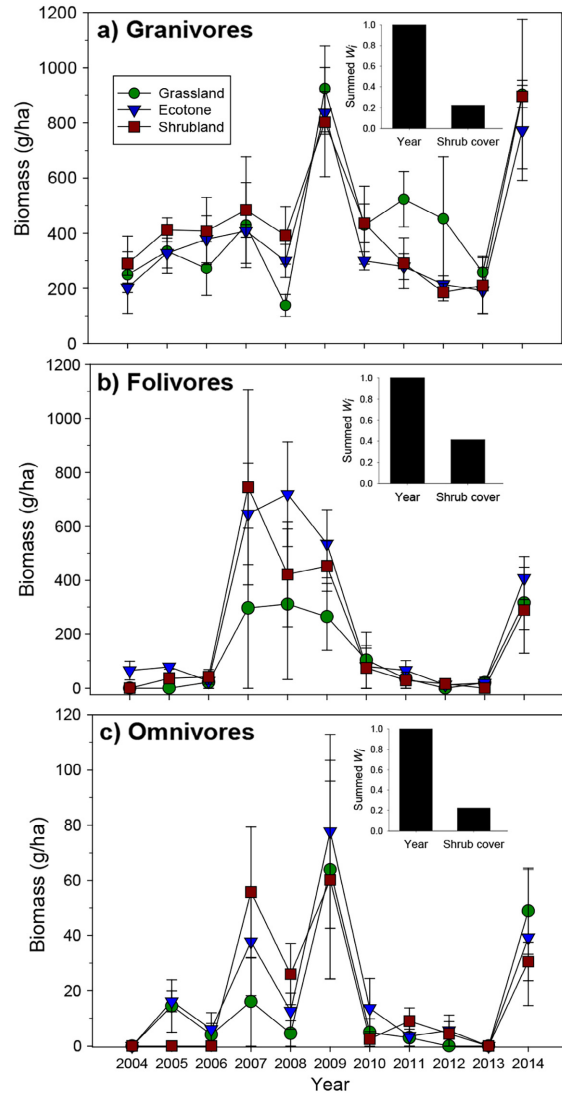


Fig. 5. Biomass dynamics of three trophic groups of desert rodents at Jornada Basin Long Term Ecological Research site: a) granivores, b) folivores, and c) omnivores. Means (± 1 standard error) are from three spatial blocks for each ecological state. Note the different y-axis for omnivores. The species assigned to each trophic group are given in Table 1. Insets indicate support for models including year or shrub cover as predictors (see Appendix S2: Table S2).

in 2007 and maintained high biomass production for two subsequent years (Fig. 5).

Collectively, our results indicate that shrub encroachment into grasslands does not create degraded habitats for Chihuahuan Desert rodents at the local scale. Total abundance of rodents and biomass of folivores increased with shrub cover, and none of the other metrics showed consistent decreases with shrub cover. Hence, our long-term monitoring supports the conclusion that shrub encroachment has no persistent negative effects on abundance and biomass of rodents (Whitford 1997, Hernández et al. 2005, Báez et al. 2006, Ernest et al. 2008, Lightfoot et al. 2012).

One major caveat is required, however, regarding shrub encroachment and degraded landscapes for desert rodents and other biodiversity elements (Eldridge et al. 2011, Stanton et al. 2017). Such assessments depend on spatial scale. Although transitions to shrublands may not reduce alpha diversity or community biomass at a local scale, this change is consequential for species such as *D. spectabilis* at regional scales due to the extensive loss and fragmentation of desert grasslands (Whitford 1997, Cosentino et al. 2014). Gamma diversity can be threatened despite the lack of clear degradation effects at local scales.

LAGGED RODENT RESPONSES TO PULSES ACROSS ECOLOGICAL STATES

We expected measures of net primary production to be better predictors of rodent biomass than precipitation because productivity is a closer link in the bottom-up chain. Most previous research used surrogates for primary production such as counts or cover of plants (Thibault et al. 2010, Hernández et al. 2011), however, so this premise remains largely untested (but see Lightfoot et al. 2012). We also predicted a time lag in any bottom-up regulation. Rodent responses to precipitation and resulting productivity pulses can be delayed because it requires time for increased reproduction and survival across seasons to play out. Although such time lags have been documented, the lengths have been variable (Báez et al. 2006, Thibault et al. 2010, Hernández et al. 2011, Lightfoot et al. 2012).

First, we evaluated evidence for time lags in how precipitation and plant productivity affect

total rodent biomass. As before, the current water year for precipitation included summer and winter seasons. We constructed repeated-measures mixed models in which we compared time lags of zero (t), 1 yr ($t - 1$), and 2 yr ($t - 2$) for predictors of rodent biomass (summer precipitation, winter precipitation, summer + winter precipitation, total ANPP, annuals ANPP). Models included fixed effects for spatial block and sampling time (early or late). Overall, models with a 1-yr time lag had the strongest support (Appendix S2: Table S3). Rodent biomass responded positively to rainfall and plant productivity measured during the previous water year. Most weight of evidence (Akaike weights, $w_i = 0.74-1.00$) was for a 1-yr lag except for annuals ANPP for which support was split between a 1-yr lag and no lag (Appendix S2: Table S3). Because neither measure of annual ANPP received support in our subsequent modeling (all $w_i < 0.01$), we used predictors with 1-yr lags for our analyses of rodent biomass.

Lightfoot et al. (2012) analyzed a different long-term data set from the Jornada Basin LTER site and found no strong relationships between rodent abundance or biomass and precipitation, but rodents responded to production of annual grasses on a grassland site (with no lag) and on a creosotebush shrubland site (1–2 yr lag). Their system was unusual, however, in that each habitat was dominated by a single species with differing reproduction potentials. At Sevilleta LTER in New Mexico, Báez et al. (2006) concluded that rodent densities responded most strongly to summer precipitation with a 1-yr time lag. At Mapimí Biosphere Reserve in northern Mexico, rodent densities and biomass measured during fall also responded to precipitation and plant cover with a 1-yr time lag (Hernández et al. 2011). Rodent densities during spring at Mapimí were related to precipitation for the current year. The narrative for the classic, long-term study at Portal, Arizona has evolved over time. An inability to detect clear links between rodent abundances and precipitation (Ernest et al. 2000, Brown and Ernest 2002) gave way to a demonstration of precipitation as a predictor of both rodent abundance and energy use (Thibault et al. 2010) with variable time lags (6–12 month lag for granivores and folivores, 1-yr lag for insectivores). Thus, our results do not rule out subtle

differences in time lags among rodent species (Lightfoot et al. 2012), but they indicate a consistent 1-yr lag in bottom-up effects at the community level, which has been witnessed in other Chihuahuan Desert systems.

Next, we developed a candidate set of models for total rodent biomass that included the lagged predictors (summer precipitation, winter precipitation, summer + winter precipitation, total ANPP, annuals ANPP) by themselves, combined with shrub cover as an additive effect, and with shrub cover as an interactive effect (Appendix S2: Table S4). We ran repeated-measures mixed models with spatial block and time of sampling as fixed effects and an autoregressive (1) covariance structure. There was only one competitive model for predicting total rodent biomass (Appendix S2: Table S4), and it included lagged summer precipitation, shrub cover, and a positive interaction between summer precipitation and shrub cover ($\beta = 0.348$, $SE = 0.103$). Rodent biomass responded more strongly to increased precipitation on shrubbier sites (Fig. 6).

This interaction has large implications for understanding how biomass production differs across ecological states, and how climate change could affect these dynamics. Following years with typical summer precipitation, rodent

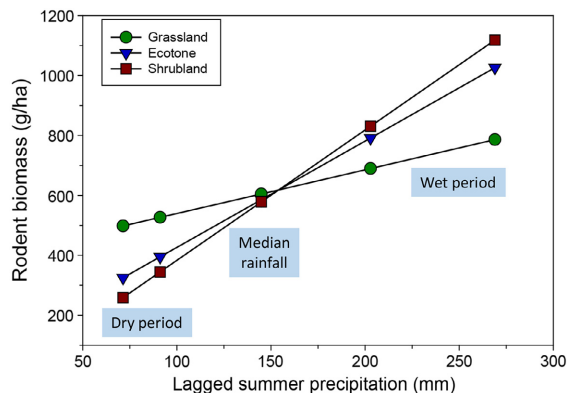


Fig. 6. Interactive effects of summer precipitation (1-yr lag) and shrub encroachment on total rodent biomass at Jornada Basin Long Term Ecological Research site. Predicted biomass is from the most supported mixed model (see Appendix S2: Table S4). For each ecological state, shrub cover was held to its mean value. The symbols represent the 10th, 25th, 50th, 75th, and 95th percentiles for summer precipitation.

biomass is similar for all three ecological states (Fig. 6). Following dry years, however, predicted biomass is greater on grasslands than on shrubbier sites (Fig. 6). This outcome partly reflects the ability of *Dipodomys spectabilis*, a large species and larder hoarder that caches substantial amounts of seeds and grass tufts within its mound (Schroder 1979), to maintain abundances relatively well during droughts. For instance, the abundance of *D. spectabilis* only decreased 37.5% from the peak year of 2009 to 2012, which ended a multi-year dry period (Fig. 4c). In contrast, during the same period the medium-sized *Dipodomys merriami* decreased by 69.1%, and the smaller *Chaetodipus eremicus* decreased by 74.8%. Following wet years, predicted rodent biomass is greater on shrubbier sites than on grasslands (Fig. 6). This response partly reflects irruptions of *C. eremicus* and transient dynamics of folivores (see *Transient dynamics and drought refugia*).

The longer-term outcome of these dynamics depends on annual variability in summer precipitation. Across our 11-yr study, the production of rodent biomass was similar on shrublands (63.9 kg) and ecotones (63.7 kg) and slightly less on grasslands (58.0 kg). Increased variability in precipitation due to climate change could result in fewer years with equal biomass across ecological states. Biomass of Chihuahuan Desert rodents should be higher in grasslands during droughts, which are predicted to become more common in the Southwest (Cook et al. 2015, Prein et al. 2016), and higher in mesquite shrublands during wet periods. Overlaid on these effects of climate change are ongoing, directional increases in shrub cover that could accelerate if shrubs respond favorably to increased precipitation variability (Gherardi and Sala 2015). Hence, expectations regarding production of rodent biomass across ecological states become less certain for the future given the complexities of climate change and landscape dynamics (Thibault et al. 2010).

DO TROPHIC GROUPS RESPOND SIMILARLY TO BOTTOM-UP PULSES?

Here, we dissect the overall response by rodents and ask whether granivores and folivores react to resource pulses in the same way. We excluded omnivores because they contributed relatively little to biomass (Fig. 5). We

anticipated that biomass of both granivores and folivores would be related more strongly to net primary production than to precipitation. However, we predicted granivores would respond strongest to ANPP of annual grasses and forbs that should reflect relevant seed production for these heteromyid rodents (Hope and Parmenter 2007, Lightfoot et al. 2012). In contrast, we predicted folivores would respond strongest to total ANPP that includes herbaceous production by all species plus cacti that is common in diets of woodrats (Hope and Parmenter 2007).

We evaluated the identical candidate set of mixed models, developed above for total rodent biomass, for both trophic groups (Appendix S2: Table S5). The best predictors for biomass of granivores and folivores were remarkably different. For granivores, all models with strong support included lagged total ANPP (Table 2; summed $w_i = 0.94$), and the top model included only this predictor. One other competitive model also included shrub cover, but model fit was not substantially improved (Table 2). Surprisingly, models with ANPP of annuals had no support for granivores (Appendix S2: Table S5). Hence, biomass of granivorous rodents was explained best by total plant production from the previous year (Fig. 7a). In contrast, all models with any support for folivores included lagged summer precipitation (Table 2; summed $w_i = 0.95$) instead of total ANPP. The only competitive model for folivores (Table 2) also included shrub cover and a positive

interaction between summer precipitation and shrub cover ($\beta = 0.169$, $SE = 0.052$). Biomass of folivores was always low following dry years, but their biomass increased more strongly on shrubier sites after wet years (Fig. 7b). This sharp difference in how bottom-up pulses drive biomass of granivores and folivores can be understood in terms of core-transient structuring of desert rodent communities (Supp et al. 2015).

TRANSIENT DYNAMICS AND DROUGHT REFUGIA

The framework for viewing communities as being composed of core species and transient species is a temporal analog of the core-satellite hypothesis (Magurran and Henderson 2003, Coyle et al. 2013). In core-transient communities, species designations are based on the temporal patterns of site occupancy. Core species are present on sites during most years, whereas transient species only occur occasionally. Transient species could be of two general types: species that exhibit source-sink dynamics in which they are a core species at other sites, or nomadic transients that track shifting resources across the landscape (Supp et al. 2015). Core species should be strongly tied to local habitat conditions (Coyle et al. 2013), and they exhibit shared life-history traits including relatively low reproductive efforts, low movement rates, and high ecological specialization (Supp et al. 2015). In contrast, dynamics of transient species should depend more on the regional species pool and

Table 2. Model selection statistics for repeated-measures mixed models evaluating predictors for biomass (g/ha) of two trophic groups of Chihuahuan Desert rodents at Jornada Basin Long Term Ecological Research site, 2006–2014.

Trophic group	Model	ΔAIC_c	w_i	$-2LL$
Granivores	Total ANPP ($t - 1$)	0	0.582	1131.0
	Total ANPP ($t - 1$), Shrub cover	1.5	0.275	1130.1
	Total ANPP ($t - 1$), Shrub cover, Total ANPP ($t - 1$) \times Shrub	3.9	0.083	1129.9
	Summer precipitation ($t - 1$)	7.0	0.018	1138.0
Folivores	Summer precipitation ($t - 1$), Shrub cover, Summer \times Shrub	0	0.839	1095.9
	Summer precipitation ($t - 1$), Winter precipitation ($t - 1$), Shrub cover, Summer \times Shrub, Winter \times Shrub	5.0	0.069	1095.7
	Summer precipitation ($t - 1$)	5.8	0.046	1106.3

Notes: Models within the 95% confidence set are presented. Summer precipitation (May–October), winter precipitation (November–April), total aboveground net primary production (ANPP), and annuals ANPP (annual grasses and forbs) were measured with a 1-yr time lag ($t - 1$). Pasture was a design variable included in all models as a spatial block. Sampling time was included as a covariate in all models to indicate whether rodent sampling occurred in mid-summer or early fall. ΔAIC_c = difference between model AIC_c and AIC_c for top model; w_i = Akaike weight; $-2LL$ = $-2(\log\text{-likelihood})$; AIC_c = corrected Akaike's information criterion.

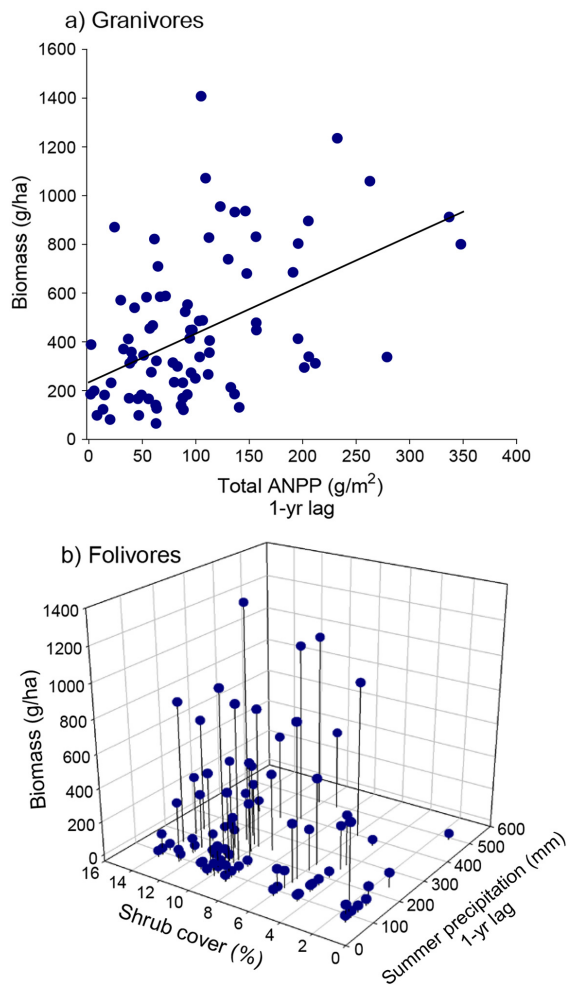


Fig. 7. Bottom-up processes differed between trophic groups of desert rodents. (a) Granivore biomass was predicted by total aboveground net primary production (ANPP) with a 1-yr lag. (b) Folivore biomass was predicted by summer precipitation with a 1-yr lag that interacted with shrub cover.

landscape heterogeneity that determine colonization potential (Coyle et al. 2013).

Because of our interest in how bottom-up regulation changes with shrub encroachment, we designated species for each ecological state in three ways (Table 1). Core species were present on an ecological state in >50% of the years. Internal transients were present on an ecological state <50% of the years, but they were a core species for another ecological state. External transients were present <50% of the years on all three ecological states. That is, external transients were

only periodically present on any of our study sites and thus they recolonized our grassland–mesquite system from elsewhere (Coyle et al. 2013, Supp et al. 2015).

Most of the granivorous rodents were core species including *Chaetodipus eremicus* and *Dipodomys ordii* that occurred on all ecological states in all years (Table 1). Even the shrub-avoiding *Dipodomys spectabilis* was a core species for shrublands because it occurred most years on the shrubland site in pasture 9 that had relatively high cover of perennial grasses (Appendix S1: Fig. S1). In contrast, the folivores included one core species, one internal transient, and one external transient (Table 1). Likewise, for the desert rodent community at Portal, Arizona, only one of the four folivore species was designated as a core species (Supp et al. 2015). In our study, *Sigmodon hispidus* was the only external transient that contributed substantial biomass (Fig. 3). The omnivores included one core species, *Onychomys leucogaster*, and four external transient species that never contributed much biomass (Table 1, Fig. 3).

We next investigated the transient dynamics of *S. hispidus*, including where it could occur outside of our system, and the consequences of transient species to biomass production during wet and dry periods. Between 2004 and 2006, *S. hispidus* was only captured on a single site in one year (Fig. 8a). However, following the extremely high summer rainfall of 2006 (Fig. 4c), *S. hispidus* was present on nearly all sites in 2007 and remained on sites for three years (Fig. 8a) driving the biomass patterns for folivores (Fig. 5b). The species then disappeared again for four years during an extended dry period before recolonizing most sites in 2014 when the drought broke. We hypothesized that the refuge habitat for *S. hispidus* during droughts was playas, which are ephemerally flooded areas located in the low zones of catchments (McKenna and Sala 2016). The vegetation of playas is often dominated by tobosa grass (*Pleuraphis mutica*), vine-mesquite grass (*Panicum obtusum*), and sometimes an assemblage of shrubs and sub-shrubs in smaller playas, and the playa fringe habitat can be dominated by mesquite even in large playas (Whitford 1976). Temporal variability of primary productivity could drive spatial dynamics of transients such as *S. hispidus* (Fernández et al. 2016). During dry periods, the mean ANPP of playas (172 g/m²) is greater than

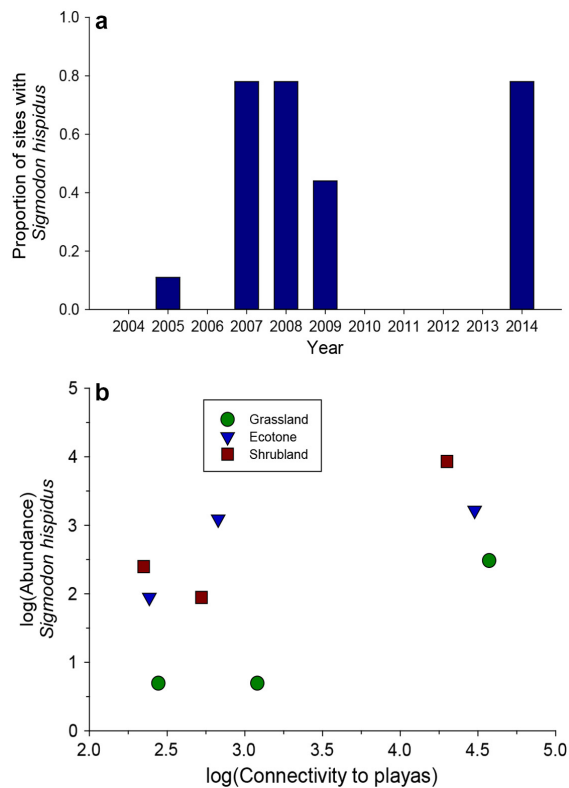


Fig. 8. Transient dynamics of the hispid cotton rat (*Sigmodon hispidus*). (a) Proportion of study sites in which *S. hispidus* was captured each year. (b) Total abundance of *S. hispidus* was predicted by spatial connectivity to playa habitats and shrub cover. Each symbol represents a study site.

the primary production for grasslands (92 g/m²) and mesquite shrublands (77 g/m²; Peters et al. 2012). *Sigmodon hispidus* has been captured in playa habitat at Jornada Basin during multiple years in which the species was absent from nearby, upland shrublands (Whitford 1976). Therefore, we predicted that our study sites close to playas, especially larger ones, should have the highest abundances of *S. hispidus*. For each site, we estimated a playa connectivity metric that was a version of simple proximity index (Gustafson and Parker 1992). For all playas within an 8-km buffer, we measured the edge-to-edge distance between the rodent trapping grid and the playa. The connectivity metric equaled the perimeter of the playa divided by the squared distance, summed for all playas within the buffer. We then constructed a generalized linear model using a

Poisson error distribution with total abundance of *S. hispidus* across the 11 yr as the response variable and playa connectivity (log-transformed) and shrub cover as predictors (GENMOD Procedure, SAS Institute 2013). Abundance of *S. hispidus* was related to playa connectivity (Wald $\chi^2 = 30.3$, $P < 0.0001$) and shrub cover (Wald $\chi^2 = 43.3$, $P < 0.0001$). When *S. hispidus* colonized our sites, abundances were higher on sites more connected to playa habitats and with greater shrub cover (Fig. 8b). Hence, the transient dynamics depended on landscape context plus habitat selection by the transient species.

Without further study, we cannot confirm our hypothesis that playas serve as refuges during drought for *S. hispidus*, although it seems likely. We also do not know whether *S. hispidus* exhibits source–sink dynamics with playas serving as source habitats, or whether the species is a nomadic transient (Supp et al. 2015) perhaps due to the periodic flooding of playas. Given that *S. hispidus* responds with a 1-yr time lag, source–sink dynamics could be at play in which playa habitats become saturated by *S. hispidus* following years with high precipitation and surplus individuals then spread out to secondary habitats.

Despite these uncertainties, the overall effect of transient species on rodent biomass can be substantial but differs greatly following wet and dry years. For example, when biomass peaked in 2007 (Fig. 4b), transient species (internal and external) produced 20–30% of the biomass on ecological states. In contrast, in 2012 following an extended dry period, transient species produced none of the rodent biomass. All biomass in 2012 was produced by core species. Hence, internal transients are restricted to their core ecological states during droughts, and external transients disappear from our grassland–mesquite system.

The historical focus of desert rodent community research was on local resource abundance, niche partitioning, and interspecific competition (Kelt 2011, Stevens and Tello 2012). However, evidence is building for the general importance of spatial dynamics for small mammals in arid and semiarid environments worldwide. Even at the Portal site in Arizona, where there was a long history of documenting local-scale competition among species (Heske et al. 1994), transient species are not rare (Supp et al. 2015) and colonization by a new species (*Chaetodipus baileyi*)

counteracted local extinctions (Ernest and Brown 2001) and contributed to zero-sum dynamics (Ernest et al. 2008). Moreover, transient dynamics related to precipitation variability as observed in our study occur in other landscapes. For instance, in thorn scrub habitat in north-central Chile where precipitation is strongly influenced by El Niño Southern Oscillation (ENSO) events, transient species are only present after heavy rains (Milstead et al. 2007, Meserve et al. 2011). The drought refugium for the transient species (*Oligoryzomys longicaudatus* and *Oligoryzomys longipilis*) is more mesic habitat near streams (aguadas). In the Simpson Desert of central Australia, rodent species also contract to refuge habitat during droughts (Dickman et al. 2011, Pavey et al. 2014). *Pseudomys australis* exhibits transient dynamics with core habitat located in cracking clay plains that receive run-on after small rain events and support ephemeral plants (Pavey et al. 2014).

CORE-TRANSIENT STRUCTURE AND TROPHIC RESPONSES

We now return to our striking result that granivore biomass was predicted by lagged plant production on a site, whereas folivore biomass was predicted by lagged summer precipitation (interacting with shrub cover). This outcome can be explained via an understanding of core-transient

dynamics. Most granivores were core species (Table 1) that should respond most strongly to local habitat conditions (Coyle et al. 2013) given their ecological specialization and low movement rates (Supp et al. 2015). Hence, it makes sense that granivorous rodents would respond to primary productivity at the local scale. In contrast, two of the three folivore species were transient species that expand and contract their distributions between core areas and secondary habitats. These transient species should respond to general landscape conditions (Coyle et al. 2013) that are indexed by broad patterns for summer precipitation. Wet years trigger spillover dynamics into secondary habitats (Céré et al. 2015). In sum, both granivores and folivores exhibit lagged responses to resource pulses but the bottom-up mechanisms differ for the two trophic groups.

CONCLUSIONS AND NEXT STEPS

Our research at the Jornada Basin LTER site highlights the importance of long-term studies for understanding how communities respond to environmental change (Hughes et al. 2017). We took advantage of repeated wet and dry periods to discern how rodent consumers react to resource pulses across ecological states representing shrub expansion in the Chihuahuan Desert (Fig. 9). Encroachment did not create a

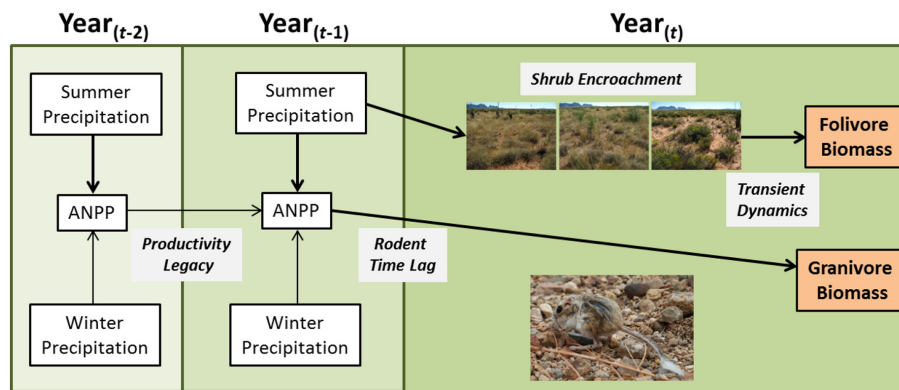


Fig. 9. A conceptual model of how resource pulses translate into biomass of Chihuahuan Desert rodents with time lags across shrub gradients. The processes for the current water year (t) and previous water year ($t - 1$) are derived from our study. The legacy effect for aboveground net primary productivity (ANPP) at a local scale was established by Sala et al. (2012). During drought periods, which are predicted to increase with climate change, transient dynamics of folivores mediated by shrub encroachment are greatly diminished. Granivores that are core species such as *Dipodomys spectabilis* contribute most of the biomass during droughts.

degraded landscape characterized by reductions in total primary productivity or rodent biomass, but this outcome could be vulnerable to climate change and a future with more droughts in the southwestern United States. We also demonstrated how core-transient processes contribute to bottom-up regulation for desert rodents in dynamic drylands. Future research should focus on how the spatial heterogeneity of primary productivity among habitats connected by dispersal (Fernández et al. 2016) drives metapopulation dynamics of transient species and promotes spatial subsidies.

Our study and previous research on Chihuahuan Desert rodents have concentrated on bottom-up processes with much less emphasis on top-down control, which can be difficult to evaluate. However, predators can exert top-down pressure on small mammals in other arid ecosystems (Henke and Bryant 1999, Moseby et al. 2009, Letnic et al. 2011). Switching trophic controls can occur in which top-down regulation is manifested only following resource pulses and prey irruptions, whereas bottom-up regulation predominates during dry periods (Meserve et al. 2003, Letnic et al. 2011). Moreover, shrub encroachment could alter predator abundance (Blaum et al. 2007) and perceived predation risk for desert rodents (Laundré et al. 2014). Ultimately, it will be necessary to integrate bottom-up dynamics with real and perceived predation risk to comprehend the full consequences of landscape change for these consumers. Nonetheless, our results and those of other studies in global drylands suggest future changes in rodent community dynamics can be predicted by combining information on lagged responses to precipitation and net primary production with core-transient structuring.

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