Let's keep brainstorming title ideas. I don't think our results support the idea of 'episodes of rapid expansion'

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Abstract

Encroachment[1] of shrubs into adjacent grasslands has become an increasingly reported phenomenon across the world, and such encroachment is either pulled forward by high population growth at the low-density encroachment front or pushed forward by higher-density areas behind the front. However, at sites such as Sevilleta National Wildlife Refuge in central New Mexico, little is known about whether encroachment is pushed or pulled, and the dynamics of encroachment are not well-understood. Here, long-term encroachment of creosotebush (Larrea tridentata), a native perennial shrub, stands in stark contrast with the stagnation in encroachment observed in recent decades. In order to better understand creosotebush encroachment at this site, we quantify it using a spatially structured population model where a wave of individuals travels at a speed governed by both dispersal and density-dependence. Results indicate that population growth rates generally increase with decreasing density, suggesting that encroachment is pulled by individuals at the low-density wave front, and the spatial population model predicts an encroachment rate of less than 2 cm per year. While the predicted rate of encroachment is consistent with observations over recent decades, it does not explain long-term creosotebush encroachment at the study site, suggesting that this process may occur in pulses when recruitment, seedling survival, or dispersal significantly exceed typical rates. Overall, our work demonstrates that individuals at low densities are likely the biggest contributors to creosotebush encroachment at this site, and that this encroachment is likely a process that occurs in large but infrequent bursts rather than at a steady pace.

Keywords

density-dependence, ecotones, woody encroachment, shrubs, integral projection model, grassland

[1] *I am not editing the abstract for now.*

Introduction

The recent and ongoing encroachment of shrubs and other woody plants into adjacent grasslands has caused significant vegetation changes across arid and semi-arid landscapes worldwide (Van Auken, 2000, 2009; Goslee et al., 2003; Gibbens et al., 2005; Parizek et al., 2002; Cabral et al., 2003; Trollope et al., 1989; Roques et al., 2001). The process of encroachment generally involves increases in the number or density of woody plants in both time and space (Van Auken, 2000), which can drive shifts in plant community structure and alter ecosystem processes (Schlesinger et al., 1990; Ravi et al., 2009; Schlesinger and Pilmanis, 1998; Knapp et al., 2008). Other effects of encroachment include changes in ecosystem services (Reed et al., 2015; Kelleway et al., 2017), declines in biodiversity (Ratajczak et al., 2012; Sirami and Monadjem, 2012; Brandt et al., 2013), and economic losses in areas where the proliferation of shrubs adversely affects grazing land and pastoral production (Mugasi et al., 2000; Oba et al., 2000).

Woody plant encroachment can be studied through the lens of spatial population biology as a wave of individuals that may expand across space and over time (Kot et al., 1996; Neubert and Caswell, 2000; Wang et al., 2002; Pan and Lin, 2012). Theory predicts that the speed of wave expansion depends on two processes: local demography and dispersal of propagules. First, local demographic processes include recruitment, survival, growth, and reproduction, which collectively determine the rate at which newly colonized locations increase in density and produce new propagules. Second, colonization events are driven by the spatial dispersal of propagules, which is commonly summarized as a probability distribution of dispersal distance, or "dispersal kernel". The speed at which expansion waves move is highly dependent upon the shape of the dispersal kernel, especially long-distance dispersal events in the tail of the distribution (Skarpaas and Shea, 2007). Both demography and dispersal may depend on plant size, since larger plants often have improved demographic performance and release seeds from greater heights,

leading to longer dispersal distances (Nathan et al., 2011). Accounting for population structure, including size structure, may therefore be important for understanding and predicting wave expansion dynamics (Neubert and Caswell, 2000).

Theory predicts that the nature of conspecific density dependence is another critical feature of expansion dynamics but this is rarely studied in the context of woody plant encroachment. Expansion waves typically correspond to gradients of conspecific density – high in the back and low at the front – and demographic rates may be sensitive to density due to intraspecific interactions like competition or facilitation. If the demographic effects of density are strictly negative due to competitive effects that increase with density then demographic performance is maximized as density goes to zero, at the leading edge of the wave. Under these conditions, the wave is "pulled" forward by individuals at the low-density vanguard (Kot et al., 1996), and targeting these individuals and locations would be the most effective way to slow down or prevent encroachment (cite?). However, woody encroachment systems often involve positive feedbacks whereby shrub establishment modifies the environment in ways that facilitate further shrub recruitment. For example, woody plants can modify their micro-climates in ways that elevate nighttime minimum temperatures, promoting conspecific recruitment and survival for freeze-sensitive species (D'Odorico et al., 2010; Huang et al., 2020). Such Allee effects (in the language of population biology) cause demographic rates to be maximized at higher densities behind the leading edge, which "push" the expansion forward, leading to qualitatively different dynamics (Kot et al., 1996; Taylor and Hastings, 2005; Sullivan et al., 2017; Lewis and Kareiva, 1993; Veit and Lewis, 1996; Keitt et al., 2001). Pushed expansion waves generally have different shapes (steeper density gradients) and slower speeds than pulled waves (Gandhi et al., 2016), and may require different strategies for managing or decelerating expansion (check Taylor and Hastings ref). The potential for positive feedbacks is well documented in woody encroachment systems but it remains unclear whether and how strongly these feedbacks decelerate shrub expansion and influ-

ence strategies for management of woody encroachment. Despite decades of work on this topic, we still do not know whether expansion waves of woody encroachment are pushed or pulled.

In this study, we linked woody plant encroachment to ecological theory for invasion waves, with the goals of understanding how seed dispersal and density-dependent demography drive encroachment, and determining whether the encroachment wave is pushed or pulled. Throughout the aridlands of the southwestern United States, shrub encroachment into grasslands is well documented (cite) but little is known about the dispersal and demographic processes that govern it. Our work focused on encroachment of creosotebush (*Larrea tridentata*) in the northern Chihuahuan Desert. Expansion of this species into grasslands over the past 150 years has been well documented, leading to decreased cover of *Bouteloua eriopoda*, the dominant foundation species of Chihuahuan desert grassland (Gardner, 1951; Buffington and Herbel, 1965; Gibbens et al., 2005). As in many woody encroachment systems, creosotebush expansion generates ecotones marking a transition from dense shrubland to open grassland, with a transition zone in between where shrubs can often be found interspersed among grasses (Fig. 1).

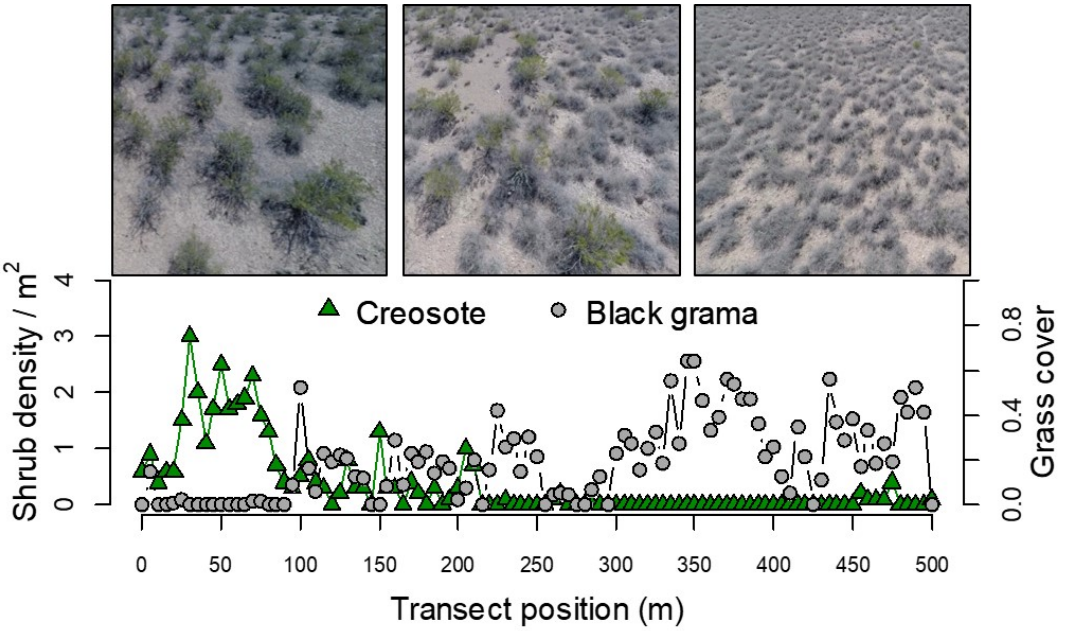

Figure 1: Caption.

Historically, creosotebush encroachment into grasslands is believed to have been driven by a combination of factors including overgrazing, drought, variability in rainfall, and suppression of fire regimes Moreno-de las Heras et al. (2016). These shrubs are also thought to further facilitate their own encroachment through positive feedbacks (Grover and Musick, 1990; D'Odorico et al., 2012) by modifying their environment in ways that favor continued growth and recruitment, such as the local micro-climate (D'Odorico et al., 2010) and rates of soil erosion (Turnbull et al., 2010). Such positive feedback also involve suppression of herbaceous competitors, reducing competition as well as the amount of flammable biomass used to fuel the fires that keep creosotebush growth in check (Van Auken, 2000). We hypothesized that, given potential for positive feedback mechanisms, the rarity of conspecifics at the low-density encroachment front may depress demographic performance and generate pushed-wave dynamics.

We used a combination of observational and experimental data from shrub ecotones

in central New Mexico to parameterize a spatial integral projection model (SIPM) that predicts that speed of encroachment (m/yr) resulting from lower-level demographic and dispersal processes. Our data came from demographic surveys and experimental transplants along replicate ecotone transects spanning a gradient of shrub density and seed drop experiments to infer the properties of the dispersal kernel. We focused on wind dispersal of seeds as a starting point, since little is known about the natural history of dispersal in this system and the seeds lack rewards to attract animal dispersers. We also used re-surveys of permanents transects as an independent measure of encroachment that provided a benchmark against which to evaluate model predictions. The SIPM accounts for size-structured demography of creosotebush, allows us to test whether shrub expansion is pulled by the low-density front or pushed from the high-density core, and identifies the local (demographic) and spatial (seed dispersal) life cycle transitions that most strongly contribute to expansion speed[2]. We address the following specific questions:

1. What is the observed rate of creosotebush encroachment in recent past?

2. How do creosotebush size and conspecific density affect variation in demographic vital rates (survival, growth, reproduction, and recruitment) along shrub encroachment ecotones?

3. What is the wind dispersal kernel for this species and how far do seeds typically travel by wind?

4. What is the predicted rate of expansion from the SIPM and what lower-level processes most strongly govern the expansion speed?

5. Is encroachment pulled by the individuals at the front of the wave or pushed by individuals behind it?

[2] *we will need to stay consistent with the language of encroachment/expansion/invasion. For now I am swictihg a lot.*

Materials and methods

Study species

Creosotebush *Larrea tridentata* is a perennial, drought-resistant shrub that is native to the arid and semiarid regions of the southwestern United States and northern Mexico. High-density areas of creosotebush consist largely of barren soil between plants due to the "islands of fertility" these shrubs create around themselves (Schlesinger et al., 1996; Reynolds et al., 1999), though lower-density areas will often contain grasses in the intershrub spaces (Fig. 1). In our northern Chihuahuan desert study region creosotebush reproduces sexually, with numerous small yellow flowers giving rise to highly pubescent spherical fruits several millimetres in diameter; these fruits consist of five carpels, each of which contains a single seed. Seeds are dispersed from the parent plant by gravity and wind, with the possibility for seeds to also be blown across the soil surface or transported by water runoff (Maddox and Carlquist, 1985). In other regions, this species also reproduces asexually and can give rise to long-lived clonal stands (Vasek, 1980), but this does not occur in our study region. The foliage is dark green, resinous, and unpalatable to most grazing and browsing animals (Mabry et al., 1978).

Study site

We conducted our experiments and censuses at the Sevilleta National Wildlife Refuge (SNWR), a Long-Term Ecological Research (LTER) site in central New Mexico. The refuge exists at the intersection of several eco-regions, including the Chihuahuan Desert and steppes of the Colorado Plateau. Annual precipitation is low at approximately 250 mm, with the majority falling during the summer monsoon season from June to September.

Significant creosotebush encroachment at SNWR is believed to have last occurred in the 1950's, with high shrub recruitment before and after a multi-year drought that

caused a large loss in grass cover, setting the stage for creosotebush expansion (Moreno-de Las Heras et al., 2015; Moreno-de las Heras et al., 2016). The recruitment events that facilitate creosotebush expansion are thought to be highly episodic (Peters and Yao, 2012). Given that creosotebush seedlings have been shown to establish around the time that late-summer heavy rainfall occurs (Boyd and Brum, 1983; Bowers et al., 2004), higher precipitation rates may be responsible for increased recruitment.

Encroachment re-surveys

We recorded shrub percent cover along two permanent 1000-m transects that spanned the shrub-grass ecotone, from high to low to near-zero shrub density. These surveys were conduced in summer 2001 and again in summer 2013 to document change in creosotebush abundance and spatial extent. At every 10 meters, shrub cover was recorded in nine cover classes ($<$1%, 1–4%, 5–10%, 10–25%, 25–33%, 33–50%, 50–75%, 75–95%, $>$95%). For visualization, we show midpoint values of these cover classes at each meter location for both transects and years.

Demographic data

Ecotone transects

Collection of demographic data occurred during early June of every year from 2013-2017. This work was conducted at four sites in the eastern part of SNWR (one site was initiated in 2013 and the other three in 2014), with three transects at each site (different transects than those used for re-surveys). All transects were placed along a shrubland-grassland ecotone so that a full range of shrub densities was captured: each transect spanned core shrub areas, grassland with few shrubs, and the transition between them. Lengths of these transects varied from 200 to 600 m, determined by the strength of vegetation transition since "steep" transitions required less length to capture the full range of shrub densities.

We quantified shrub density in 5-meter "windows" along each transect, including all plants within one meter of the transect on either side. Densities were quantified once for each transect (in 2013 or 2014) and were assumed to remain effectively constant for the duration of the study, a reasonable assumption for a species with very low recruitment and very high survival of established plants. Given the population's size structure, we weighted the density of each window by the sizes of the plants, which we quantified as volume (cm^3). Volume was calculated as that of an elliptic cone: $V_i = \frac{\pi h}{3}\frac{lw}{4}$ where l, w, and h are the maximum length, maximum width, and height, respectively. Maximum length and width were measured so that they were always perpendicular to each other, and height was measured from the base of the woody stem at the soil surface to the highest part of the shrub. The weighted density for a window was then expressed as log(volume) summed over all plants in the window.

Observational census

At 50-m intervals along each transect we tagged up to 10 plants for annual demographic census and recorded their local (5-m resolution) window so that we could connect individual demographic performance to local weighted density. These tagged shrubs were revisited every June and censused for survival (alive/dead), size (width, length, and height, as above), and reproduction (numbers of flowers and fruits). In instances where shrubs had large numbers of reproductive structures that would be difficult to reliably count (a large shrub may have many hundreds of flowers or fruits), we made counts on a fraction of the shrub and extrapolated to estimate whole-plant reproduction. Creosotebush does not have a discrete reproductive season, instead producing flowers and fruits over much of the warm season. Our measurements of reproductive output are therefore conservative, and likely underestimate cumulative seed production for an entire transition year. Each year, we also searched for new recruits within one m on either side of the transect. New recruits were tagged and added to the demographic census.

Transplant experiment

We conducted a transplant experiment in 2015 to test how shrub density affects seedling survival. This approach complemented observational estimates of density dependence and filled in gaps for a part of the shrub life cycle that is rarely observed due to low recruitment. Seeds for the experiment were collected from plants in our study population in 2014. Seeds were germinated on Pro-Mix potting soil (Quakertown, PA) in Fall 2014 and seedlings were transferred to 3.8 cm-by-12.7 cm cylindrical containers and maintained in a greenhouse at Rice University. Seedlings were transported to SNWR and transplanted into our experimental design during July 27-31 2015. Transplant timing was intended to coincide with the start of the monsoon season, when most natural recruitment occurs.

The transplant experiment was conducted at the same four sites and three transects per site as the observational demographic census, where we knew weight shrub densities at 5-m window resolution. Along each transect we established 12 1-m by 1-m plots. Plots were intentionally placed to capture density variation: four plots were in windows with zero shrubs, four plots were placed in the top four highest-density windows, and the remaining four plots were randomly distributed among the remaining windows with weighted density greater than zero. Plots were placed in the middle of each 5-m window (at meter 2.5). Plots were divided into four 0.5-m by 0.5-m subplots. We divided each subplot into nine squares and recorded ground cover of each square as one of the following categories: bare, creosotebush, black grama (*B. eriopoda*), blue grama (*B. gracilis*), other grass, or "other". Each subplot received one transplanted subplot, for a total of 48 transplants per transect, 144 transplants per site, and 576 transplants in the entire experiment. Each site was set up on a different day and there was a significant monsoon event after the third and before the fourth site. This resulted in differential mortality that appears to be related to site (the soil was moist at the fourth site at the time of transplanting, which favored survival) but more likely reflects the timing of the monsoon event relative to planting. We revisited the transplant experiment on October 24, 2015 to

survey mortality. After that first visit, transplants were censused along with the naturally occurring plants each June, following the methods described above.

Demographic analysis

We fit statistical models to the demographic data and used AIC-based model selection to evaluate empirical support for alternative candidate models. The top statistical models were then used as the vital rate sub-models of the SIPM, so there is a strong connection between the statistical and population modeling, as is typical of integral projection modeling. Our analyses focused on the following demographic vital rates: survival, growth, probability of flowering, flower and fruit production, and seedling recruitment. All of these except recruitment were modeled as a function of plant size, and all of them included the possibility of density dependence, since we could connect the demographic performance of individual shrubs to the weighted density of their transect window.

The alternative hypotheses of pushed versus pulled wave expansion ultimately rest on how demographic vital rates, and the rate of population increase (λ) derived from the combination of all vital rates, respond to density. We were particularly interested in whether demographic performance was maximized as local density goes to zero (pulled) or at non-zero densities behind the wave front (pushed). To flexibly model density dependence and detect non-monotic responses, we used generalized additive models in the R package 'mgcv' (Wood, 2017). For each vital rate, we fit candidate models with or without a smooth term for local weighted density (among other possible covariates). To avoid over-fitting, we set the 'gamma' argument of gam() to 1.2, which increases the complexity penalty, results in smoother fits (Wood, 2017), and makes our approach more conservative. We pooled data across transition years for demographic analysis. All models included the random effect of transect; we did not attempt to model both site and transect-within-site random effects due to the low numbers of each. All vital rate functions used the natural logarithm of volume (cm^3) as the size variable and the sum

log(volume) as the weighted density of a transect window.

Survival We modeled survival or mortality in year $t+1$ as a Bernoulli random variable with three candidate models for survival probability. These included smooth terms for initial size in year t only (1), initial size and weighted density (3), and both smooth terms plus an interaction between initial size and weighted density. We analyzed survival of experimental transplants and observational census plants together in the same analyses, with a fixed effect of 'transplant' included in all candidate models. Since recruits and thus mortality events were both very rare in the observational survey, this approach allowed us to "borrow strength" over both data sets to generate a predictive function for size and possibly density -dependent survival while statistically accounting for differences between experimental and naturally occurring plants. Because we had additional, finer-grained cover data for the transplant experiment that we did not have for the observational census, we conducted an additional stand-alone analysis of transplant survival that explored the influence of covariates at multiple spatial scales (Appendix).

Growth We modeled size in year $t+1$ as a Gaussian random variable. There were nine candidate models for growth (Table). The simplest model (1) defined the mean of size in year $t+1$ as a smooth function of size in year t and constant variance Models (2) and (3) had constant variance but the mean included smooth terms for initial size and weighted density (2) or both smooth terms plus an interaction between initial size and weighted density (3). Models 4-6 had the same mean structure as 1-3 but defined the standard deviation of size in year $t+1$ as a smooth function of initial size. Models 7-9 mirrored 4-6 and additionally included a smooth term for weighted density in the standard deviation.

Flowering and fruit production We modeled shrub reproductive status (vegetative or flowering) in year t as a Bernoulli random variable with three candidate models for

flowering probability. These included smooth terms for current size (in year t) only (1), size and weighted density (3), and both smooth terms plus an interaction between size and weighted density. We modeled the reproductive output of flowering plants (the sum of flowerbuds, open flowers, and fruits) in year t as a negative binomial random variable. There were three candidate models for mean reproductive output that corresponded to the same three candidates for flowering probability.

Recruitment We modeled seedling recruitment in each transect window as a binomial random variable given the number of seeds produced in that window in the preceding year. To estimate window-level seed production, we used the best-fit models for flowering and fruit production and applied this to all plants in each window that we observed in our initial density surveys.

Integral Projection Model

The size- and density-dependent statistical models comprised the sub-models of an Integral Projection Model that we used to evaluate how the shrub population growth rate responded to conspecific density. A basic density-independent IPM predicts the number of individuals of size $x\prime$ at time $t+1$ ($n(x\prime, t+1)$) based on a projection kernel (K) that gives the rates of transition from sizes x to $x\prime$ and is integrated over the size distribution from the minimum (L) to maximum (U) sizes. As in our statistical modeling, the size variable of the IPM ($x, x\prime$) was $log(cm^3)$. In our model, the projection kernel was additionally dependent on local density, which we represent with $\tilde{N}$.

$$n(x\prime, t+1) = \int_L^U K(x\prime, x, \tilde{N}) n(x,t)\, dx \tag{1}$$

For our model, the demographic transitions captured by the projection kernel include growth or shrinkage (G) from size x to $x\prime$, conditioned on survival (S) at size x, and the production of new size-$x\prime$ individuals from size-x parents. Reproduction reflects the

number of seeds produced at size x (F), conditioned on flowering (P), the per-seed probability of recruitment (R), and the size distribution of recruits (C). Thus, we can express the projection kernel as:

$$K(x\prime, x) = S(x, \tilde{N})G(x\prime, x, \tilde{N}) + P(x, \tilde{N})F(x, \tilde{N})R(\tilde{N})C(x\prime) \quad (2)$$

In the statistical modeling, we explored density ($\tilde{N}$) effects in all of these vital rates expect the recruit size distribution. We observed only XX natural recruits during our study, so we were not able to connect recruit size to local density. Instead, we used the pooled recruits to estimate a mean and standard deviation of recruit size assuming a Gaussian distribution.

For analysis, we evaluated the IPM kernel functions at a range of local densities ($\tilde{N}$), from the minimum to the maximum of weighted density values from the 5-meter windows. At each density level, we discretized the IPM kernel into XX bins and calculated the asymptotic growth rate $\lambda(\tilde{N})$ as the leading eignevalue of the approximating matrix. We extended the lower (L) and upper (U) integration limits to avoid unintentional "eviction" using the floor-and-ceiling method (Williams et al., 2012).

We sought to characterize the "shape" of density dependence: whether fitness declined monotonically or not with increasing density. We quantified uncertainty in the density-dependent growth rate $\lambda(\tilde{N})$ by bootstrapping our data. For each bootstrap, we randomly sampled XX% of our demographic data, re-ran the statistical modeling and model selection, and used the top vital rate models to generate $\lambda(\tilde{N})$ for that data subset. We repeated this procedure for 500 bootstrap replicates.

Dispersal modelling

Dispersal kernels were calculated using the WALD, or Wald analytical long-distance dispersal, model that uses a mechanistic approach to predict dispersal patterns of plant

propagules by wind. The WALD model, which is largely based in fluid dynamics, can serve as a good approximation of empirically-determined dispersal kernels (Katul et al., 2005; Skarpaas and Shea, 2007) and may be used when empirical dispersal data is not readily available. Under the assumptions that wind turbulence is low, wind flow is vertically homogenous, and terminal velocity is achieved immediately upon seed release, the WALD model simplifies a Lagrangian stochastic model to create a dispersal kernel that estimates the likelihood a propagule will travel a given distance (Katul et al., 2005). This dispersal kernel takes the form of the inverse Gaussian distribution

$$p(r) = \left(\frac{\lambda'}{2\pi r^3}\right)^{\frac{1}{2}} \exp\left[-\frac{\lambda'(r-\mu')^2}{2\mu'^2 r}\right] \tag{3}$$

that is a slight adaptation from equation 5b in Katul et al. (2005), using r to denote dispersal distance. Here, λ' is the location parameter and μ' is the scale parameter, which depend on environmental and plant-specific properties of the study system. The location and scale parameters are defined as $\lambda' = (H/\sigma)^2$ and $\mu' = HU/F$; these are functions of the height H of seed release, wind speed U at seed release height, seed terminal velocity F, and the turbulent flow parameter σ that depends on both wind speed and local vegetation roughness.

In order to create the dispersal kernel, we first take the wind speeds at measurement height z_m and correct them to find wind speed U for any height H by using the logarithmic wind profile

$$U = \frac{1}{H}\int_{d+z_0}^{H} \frac{u^*}{K} \log\left(\frac{z-d}{z_0}\right) dz \tag{4}$$

given in Bullock et al. (2012) equation 6, with the notation slightly modified. Here, z is the height above the ground, K is the von Karman constant, and u^* is the friction velocity. The zero-plane displacement d and roughness length z_0 are surface roughness parameters that, for a grass canopy height h above the ground, are approximated by

$d \approx 0.7h$ and $z_0 \approx 0.1h$. These estimates are from Raupach (1994) for a canopy area index $\Lambda = 1$ in which the sum of grass canopy elements is equal to the unit area being measured. A 0.15 m grass height at the study site gives $d = 0.105$ and z_0, which are suitable approximations for grassland (Wiernga, 1993). Calculations of u^* were done using equation A2 from Skarpaas and Shea (2007), in which

$$u^* = KU_m \left[\log \left(\frac{z_m - d}{z_0} \right) \right]^{-1} \tag{5}$$

and U_m is the mean wind velocity at the measurement height z_m. Values for the turbulent flow parameter σ were then calculated using the estimate made by Skarpaas and Shea (2007) in their equation A4, where

$$\sigma = 2A_w^2 \sqrt{\frac{K(z-d)u^*}{C_0 U}} \tag{6}$$

and C_0 is the Kolmogorov constant. A_w is a constant that relates vertical turbulence to friction velocity and is approximately equal to 1.3 under the assumptions of above-canopy flow made by Skarpaas and Shea (2007), based off calculations from Hsieh and Katul (1997). In addition, the assumption that $z = H$ was made in order to make the calculation of σ more feasible.

The values from the previous three equations give us the necessary information to calculate μ' and λ', thus allowing us to create the WALD distribution $p(r)$. However, the base WALD model does not take into account variation in wind speeds or seed terminal velocities, which limits its applicability in systems where such variation is present. In order to account for this variation, we integrate the WALD model over distributions these two variables using the same method as Skarpaas and Shea (2007). The WALD model assumes seed release from a single point source, though, which is not realistic for a shrub; because seeds are released across the entire height of the shrub rather than from a point source, $p(r)$ was also integrated across the uniform distribution from the grass canopy

height to the shrub height. Thus, under the assumptions that the height at which a seed is located does not affect its probability of being released and that seeds are evenly distributed throughout the shrub, this gives the dispersal kernel $K(r)$, where

$$K(r) = \iiint p(F)p(U)p(z)p(r)\,dF\,dU\,dz \tag{7}$$

and $p(F)$ and $p(U)$ are the PDFs of the terminal velocity F and wind speed U, respectively, and $p(z)$ is the uniform distribution from h to H.

The distribution $p(F)$ in the integral above was constructed using experimentally determined seed terminal velocities. This was done by using a high-speed camera and motion tracking software to determine position as a function of time, and then using the Levenberg-Marquardt algorithm to solve a quadratic-drag equation of motion for F. Before seeds were released, they were dried and then dyed with yellow fluorescent powder, and then put against a black background to improve visibility and make tracking easier. While the powder added mass to the seeds, this added mass only yielded an approximately 2.5% increase and was thus negligible, likely having little effect on their terminal velocities. Measurements were conducted for 48 seeds that were randomly chosen from a seed pool derived from different plants, and then an empirical PDF of terminal velocities was constructed using the data. Constructing $p(U)$ involved creating an empirical PDF of hourly wind speeds at Five Points, the site closest to the 12 transects being used, that were obtained from meteorological data collected at the Sevilleta National Wildlife Refuge from 1988 to 2010. We did not weight $p(U)$ and assumed that the probability seed release from the shrub is the same regardless of wind speed.

Spatial integral projection model

Given that the shrub population at this site is approximately homogeneous perpendicular to the direction of encroachment, expansion is modelled as a wave moving in one

dimension. A spatial integral projection model (SIPM) is used to estimate the speed at which encroachment occurs; such a model incorporates the effects of variation in traits like plant size that stage-structured models, such as those described in Neubert and Caswell (2000), do not capture. According to Jongejans et al. (2011), a general SIPM can be formulated as

$$\mathbf{n}(x_2, z_2, t+1) = \iint \tilde{K}(x_2, x_1, z_2, z_1)\mathbf{n}(x_1, z_1, t)\, dx_1\, dz_1 \tag{8}$$

where x_1 and x_2 are locations of individuals of a particular size before and after one unit of time, and z_1 and z_2 are the respective sizes. The vector $\mathbf{n}$ indicates the population density of each size, and $\tilde{K}$ is a kernel that combines dispersal with demography. Though this SIPM represents a continuous spectrum of shrub sizes and densities, it was implemented by discretising the above integral with a 200 x 200 matrix, as this makes calculations significantly more tractable.

Movement of the wave is determined by the components of the combined dispersal/demography kernel $\tilde{K}$, which is of the same form as that used in Jonjegans et al. (2011). Here,

$$\tilde{K}(x_2, x_1, z_2, z_1) = K(x_2 - x_1)Q(z_2 - z_1) + \delta(x_2 - x_1)G(z_2 - z_1) \tag{9}$$

and K is the dispersal kernel, Q a reproduction function, G a growth function, and δ the Dirac delta function. G is derived from the model for annual growth ratio, and Q is derived from the reproductive structures model as well as other factors including number of seeds per reproductive structure, probability of recruitment from seed, and recruit size. Both G and Q give the probability of transition between sizes; in the case of G, this is the probability of growing from one specific size to another, and in the case of Q the probability that an individual of a specific size produces a recruit of a specific size. The product of K and Q represents the production and dispersal of motile propagules, while

the product of G and δ represents the growth of sessile individuals.

Given growth function G and the reproduction function Q, the speed of the moving wave can be calculated as

$$c^* = \min_{s>0} \left[\frac{1}{s} \ln(\rho_s) \right] \tag{10}$$

where s is the wave shape parameter and ρ_s is the dominant eigenvalue of the kernel $\mathbf{H_S}$ (Jongejans et al., 2011). This estimate for the wavespeed is valid under the assumption that population growth decreases monotonically as conspecific density increases, with the highest rates of growth occurring at the lowest population densities (Lewis et al., 2006). The kernel $\mathbf{H_S}$ is defined as

$$\mathbf{H_S} = M(s)Q(z_2 - z_1) + G(z_2 - z_1) \tag{11}$$

where $M(s)$ is the moment-generating function of the dispersal kernel (Jongejans et al., 2011). For one-dimensional dispersal, this moment-generating function can be estimated as

$$M(s) = \frac{1}{N} \sum_{i=1}^{n} I_0(sr_i) \tag{12}$$

where r is the dispersal distance for each observation, and I_0 is the modified Bessel function of the first kind and zeroth order (Skarpaas and Shea, 2007). In order to obtain M, numerous dispersal distances were simulated from the dispersal kernel $K(r)$ described in the previous section, with over 2000 replications for each shrub height increment of 1 cm. This was performed over the range from the lowest possible dispersal height to the maximum shrub height. Once $M(s)$ was obtained for dispersal at each shrub height, $\mathbf{H_S}$ and c^* were calculated for each value of s; this was done for values of s ranging from 0 to 2, as it is this range in which c^* occurs.

Estimates of the wavespeed were bootstrapped for a total of 1000 replicates. Each bootstrap replicate recreated size- and density-dependent demographic models using 80%

resampling on the original demographic data, and recreated dispersal kernels also using 80% resampling on the wind speeds and seed terminal velocities. Between replicates, the structure of the demographic models was kept constant, though coefficient estimates were not; this approach, while effectively ignoring model uncertainty, has the benefit of increasing computational efficiency, which is especially useful given the time-consuming nature of numerically estimating the many dispersal kernels used in the model.

Results

Encroachment re-surveys

Figure 2.

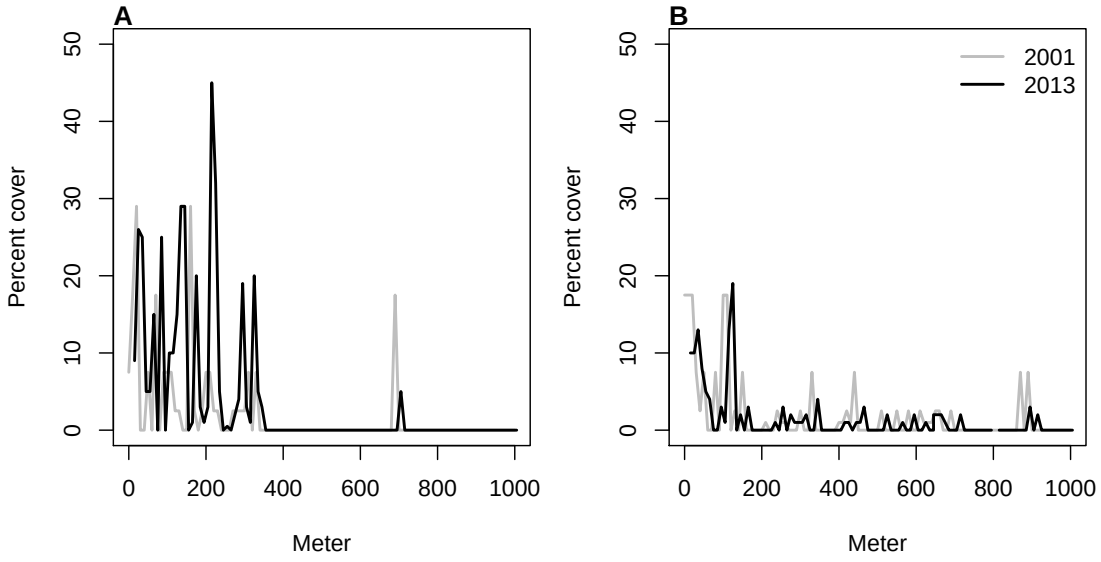

Figure 2: Re-surveys of shrub cover along two permanent trasects (A,B) surveyed in 2001 and 2013.

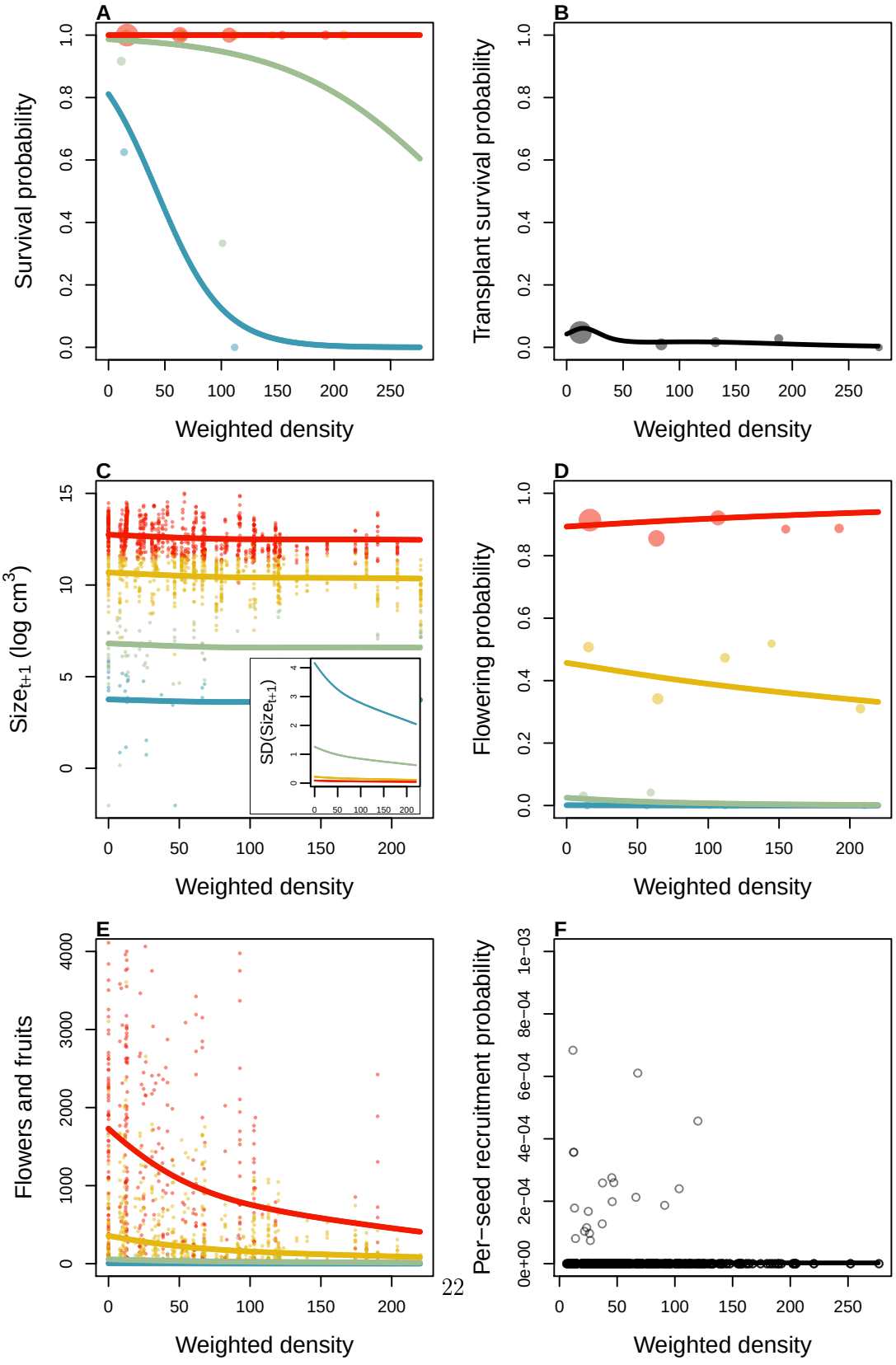

Figure 3: Size- and density-dependence in demographic vital rates.

Survival

Growth

Flowering and fruit production

Recruitment

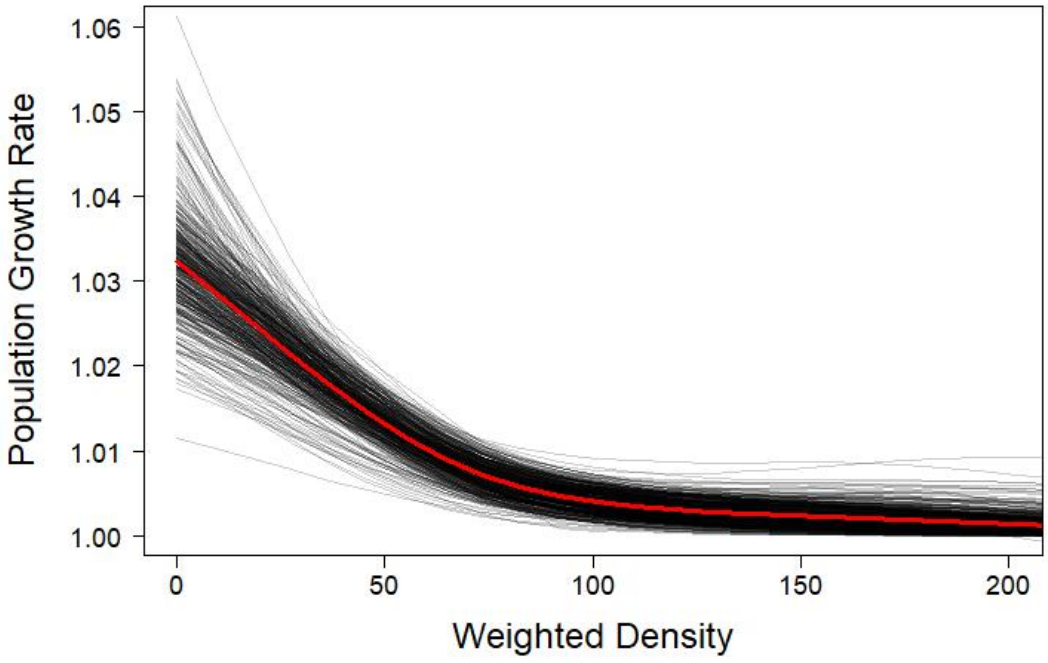

Figure 4: Density dependence in the geographic population growth rate (λ).

Population growth rate The speed of encroachment at the study site as estimated by the SIPM is rather slow; as can be seen in Figure 5, the low-density wavefront moves at approximately 0.5 cm/yr under normal conditions and at 1 cm/yr under the best seedling survival conditions observed in the dataset. These improved conditions were observed due to above-average rainfall that occurred after greenhouse-grown seedlings

were transplanted to the site. Population growth in this low-density region of the moving wave is also low, with a geometric growth rate of $\lambda \approx 1.006$ and even lower rates of growth the higher-density regions behind; in the higher-survival scenario the maximum rate increases to $\lambda \approx 1.013$, with growth still decreasing as density increases. For both scenarios, the decrease in population growth rate with increasing density was monotonic across the range of observed standardised densities, as is shown in Figure 5. This suggests that an Allee effect is likely not present in this population, as the highest rate of population growth is found at the lowest density vanguard of the encroaching population. Thus, the conditions necessary for equation 9 to be valid are satisfied, and these wavespeeds are applicable for a pulled-wave scenario in which no Allee effects are present.

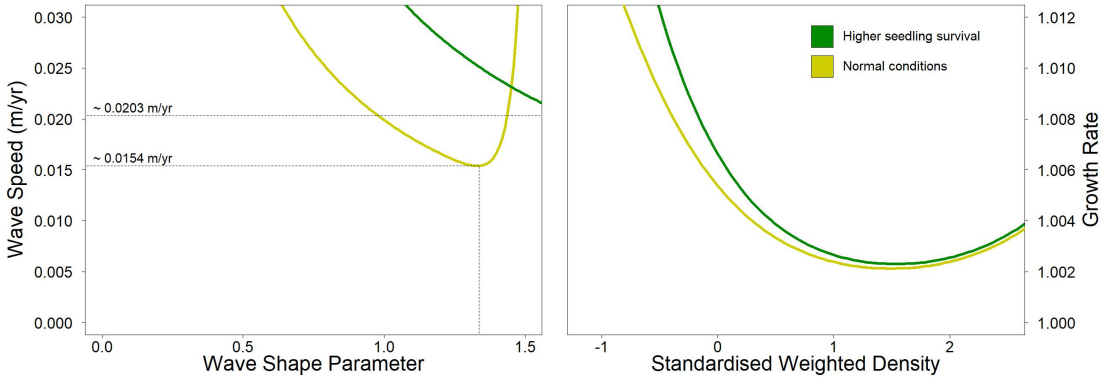

Figure 5: Estimated encroachment wave speeds (left) and geometric rates of population growth (right) for higher post-rainfall seedling survival and normal conditions.

As the speed of encroachment is quite limited, so is the extent of wind dispersal. Long distance dispersal events, while more common for taller shrubs than their shorter counterparts, are still uncommon overall. For the tallest shrub height of 1.98 m, only 0.32% of propagules exceed a dispersal distance of 5 m, and 0.02% exceed 10 m. At 1 m, or approximately half the tallest shrub height, long distance dispersal is even less likely, with 0.0046% of propagules exceeding a dispersal distance of 5 m and 0.0009% exceeding 10 m. Given that the median shrub height is only 0.64 m, the occurrence of

long-distance wind dispersal in most of the shrub population is highly improbable, and the few instances in which it occurs will only be limited to the tallest shrubs. Thus, as Figure 6 demonstrates, shorter dispersal distances dominate; even for the tallest shrub, 81% of seeds fall within only a metre of the plant, and this percentage increases as shrub height decreases. Dispersal kernels have their highest probability density at dispersal distances between 2 and 8 cm from the shrub; here, as shrub height increases, the most probable dispersal distance slightly increases while maximum probability density decreases. Regardless of the shrub height, most dispersal will occur very close to the plant, though increases in shrub height dramatically increase the likelihood of dispersal at longer distances. It is clear that the shape of the height-dependent dispersal kernel $K(r)$ varies greatly among the shrub population given the large range of shrub heights observed; shrubs at lower heights have more slender kernels with most of the seeds dispersing closer to the plant, while taller shrubs have kernels with much fatter tails and are more capable of longer-distance dispersal.

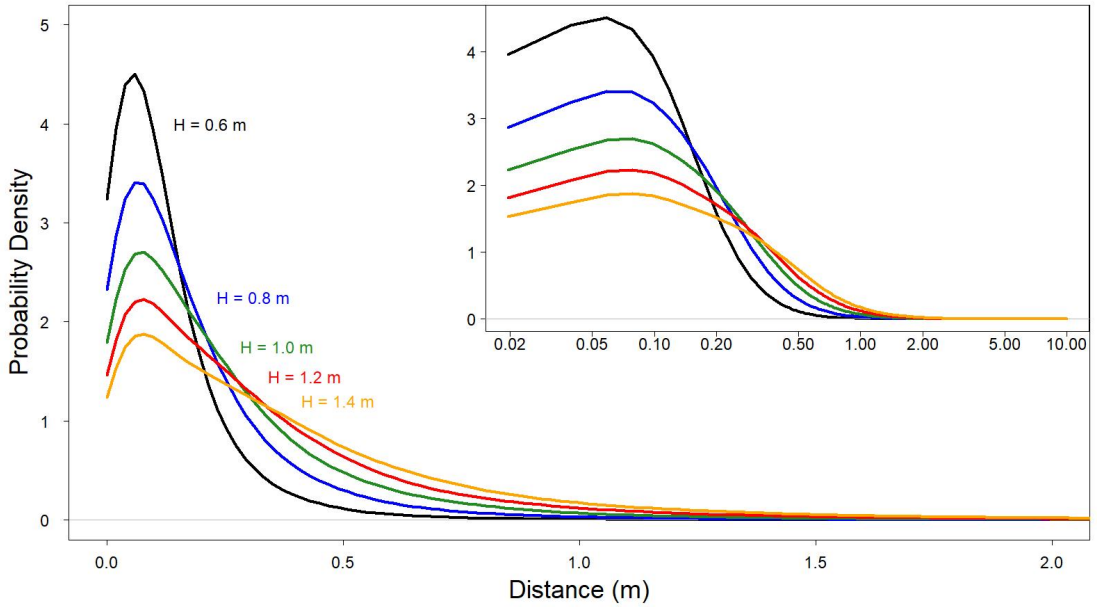

Figure 6: Dispersal kernels, with each colour representing a selected shrub height. The inset plot is the same as the large plot, though with a logarithmic x-axis to more easily show differences in dispersal probability at smaller distances.

Density and size dependence are evident in all 4 of the demographic rates, with coefficients for each model displayed in Table 2. For growth, reproduction, and survival, density dependence is mostly negative and monotonic; this is not the case for probability of flowering, where shrub size seems to be more important than the effects of density alone and suggests that larger shrubs have a higher probability of flowering than their smaller counterparts. This, along with size and density dependence in growth and reproduction, is shown in Figure 7. Size dependence is positive for reproduction, as would be expected since larger plants typically produce more flowers and fruits. However, annual growth decreases as size increases; this could be in part due to the annual growth in this study being quantified as a proportion relative to the shrub's initial size. While larger shrubs may produce more plant material over a year in terms of absolute volume, smaller shrubs produce less but can still have higher annual growth in terms of the percentage of volume

added relative to their initial volume. When compared to density, shrub size is a much stronger predictor of survival, with significant differences in mortality rates depending on shrub size. For small shrubs, mortality is exceptionally high, and increases in volume for these shrubs only slightly increase the likelihood of survival. However, after shrubs reach a logarithmic volume of approximately 7.3, they are almost guaranteed to survive, with survival rates near 100% persisting regardless of any further size increases. Interestingly, though most recruits were found at lower densities, the probability of recruitment from seed displays positive density dependence; the probability of recruitment was still very low, though, with a baseline rate of approximately 2 recruits per 10,000 seeds.

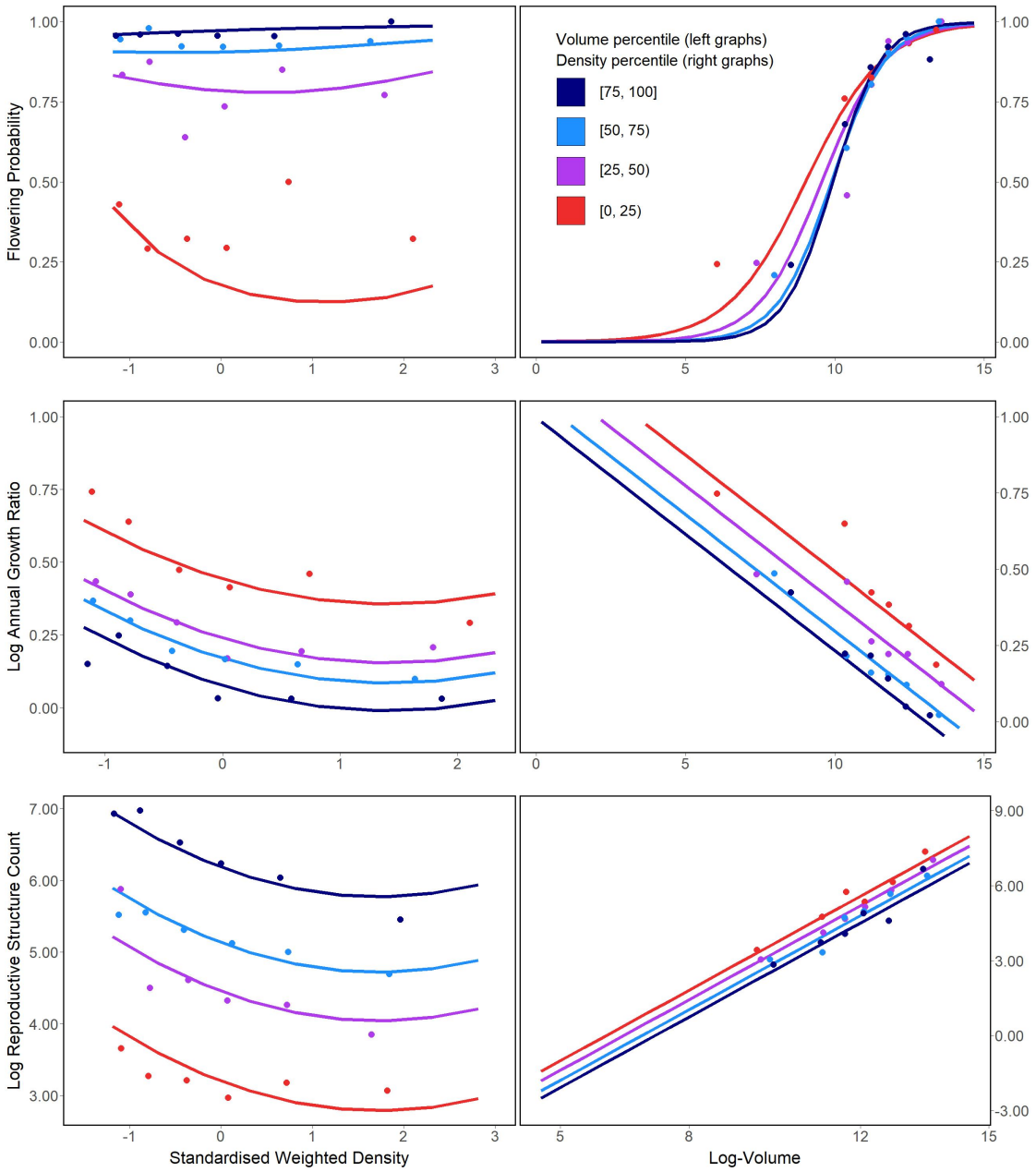

Figure 7: Flowering probability (top row), log annual growth ratio (centre row), and log reproductive structure count (bottom row) at all four sampling sites. In the left column of graphs, the three response variables are shown as a function of density for each of four volume quartiles, with each quartile containing six density bins; in the right column, the opposite occurs, with response variables shown as functions of four volume quartiles that each contain six density bins. Graphs quantifying the number of reproductive structures include data only on plants that flowered.

Discussion

The slow movement of the encroaching creosotebush wave at the Sevilleta LTER site can likely be contributed to a combination of three factors: short dispersal distances with extremely limited long-distance dispersal events, very low probability of recruitment from seed, and high seedling mortality. These three barriers, when combined, form a formidable challenge to the establishment of new shrubs at the low-density front of the wave. First, a seed must travel far enough to avoid competition with the parent shrub, which is unlikely given the dispersal kernels shown in Figure 2. Even if the seed manages to be dispersed this far, its chances of becoming a seedling are low. Caching and consumption by seed-eaters such as a variety of seed-harvesting ants (Whitford, 1978; Whitford et al., 1980; Lei, 1999) and the kangaroo rat Dipodomys merriami (Chew and Chew, 1970) decreases the amount of seeds available for germination. However, reduction in germination caused by destruction of seeds may be partly mitigated by the more favourable germination conditions that these seeds can experience when cached underground (Chew and Chew, 1970). Many of the remaining seeds will still fail to germinate, and in the unlikely event that germination does occur, seedlings will likely die given the high rates of mortality observed in smaller shrubs. Such high rates of creosotebush seedling mortality have been observed in other studies as well (Boyd and Brum, 1983; Bowers et al., 2004), probably due to a combination of herbivory, competition, and abiotic stresses.

However, as low as they are, the wavespeed estimates given in this paper are still conservative estimates for reasons mostly related to dispersal. First, it is important to note that the dispersal kernels used here, while they account for variation in factors such as wind speed and terminal velocity, may underestimate the distances that shrub propagules travel. Because the WALD model assumes that terminal velocity is reached immediately upon seed release, seeds in the estimate thus take a shorter time to fall

and have less time to be transported by wind, and the true frequency of long-distance dispersal events may thus be greater than what is estimated here. Second, dispersal at the study site could occur through additional mechanisms other than wind. For example, secondary dispersal through runoff from significant rainfall events can transport seeds (Thompson et al., 2014), and given that long-distance dispersal by bird and subsequent species divergence is thought to be responsible for creosotebush being in North America in the first place (Wells and Hunziker, 1976), short-distance dispersal by other animals at the study site likely occurs. As mentioned above, seeds are transported by seed-harvesting ants and granivorous mammals, where they are often stored in caches that can be appreciable distances from the parent shrubs. Whether transportation occurs via ant or rodent, creosotebush seeds can be moved significantly further than wind alone can, though many of these seeds are eventually consumed.

Despite the more conservative estimates our model yields, the estimated rate of dispersal in creosotebush populations at the Sevilleta National Wildlife Refuge is consistent with observations from the past 50-60 years, as creosotebush expansion during this time has been minimal (Moreno-de las Heras et al., 2016). However, it cannot explain the long-term increases in creosotebush cover at the study site, as total encroachment over the past 150 years is much greater than what would be expected given the encroachment rates derived by our models. Such a discrepancy is likely due to much of the expansion occurring in an episodic fashion, with short times during which rapid encroachment occurs due to favourable environmental conditions. This could be due in part to seedling recruitment, which is a factor that strongly limits creosotebush expansion, being rare and episodic. For example, Allen et al. (2008) estimate that a major recruitment event occurred at this site in the 1950s, which is supported by photographic evidence from Milne et al. (2003) of a drought-driven expansion during this time. Moreno-de las Heras et al. (2016) estimate that after this expansion, several smaller creosotebush recruitment events occurred in decadal episodes. However, such events can be highly localised and

may not necessarily occur at the low-density front of encroachment, which could explain how these recruitment events can still coexist with lack of encroachment in the recent past.

Overall, our observations and model highlight three aspects of creosotebush encroachment that should be the focus of future studies seeking to obtain better estimates of encroachment rates. First, negative density dependence in survival, growth, and reproduction is demonstrated, along with size dependence. The clear dependence on size and conspecific density suggests that they both should be considered when estimating creosotebush expansion and quantifying the demographic variation that contributes to it. Second, wind dispersal in these shrubs is quite limited; though the dispersal kernels seen here are typical in the sense that they are characterised by high near-plant dispersal and exceptionally low long-distance dispersal, the scale across which such dispersal occurs is small, with most seeds landing within only 1 m of the shrub. Wind dispersal alone may be an underestimate of the true amount of dispersal occurring, and future work should seek to incorporate the effects of dispersal by runoff and animals so that a more representative model of total dispersal can be obtained. Finally, encroachment is slow or even stagnates, but only most of the time. Though our encroachment speed estimates are representative of creosotebush populations for most years, the significant expansion seen over larger time scales suggests that there is episodic expansion in other years; while our model is consistent with the recent stagnation in creosotebush encroachment at the Sevilleta LTER site, a model that also includes interannual variability in factors such as survival and recruitment would be able to better account for instances of episodic population expansion that are characteristic of this location.

Acknowledgements

Author contributions

Data accessibility

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