

Spatial integral projection models predict slow
creosotebush encroachment between episodes of rapid
expansion

Trevor Drees^{*a,b}, Brad M. Ochocki^b, Scott L. Collins^c, and Tom E.X. Miller^b

^aDepartment of Biology, Penn State University, State College, PA USA

^bProgram in Ecology and Evolutionary Biology, Department of BioSciences, Rice
University, Houston, TX USA

^cDepartment of Biology, University of New Mexico, Albuquerque, NM USA

July 2, 2020

^{*}thd5066@psu.edu

1 Abstract

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

22 Keywords

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

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

25 Introduction

26 The encroachment of shrubs and other woody plants into adjacent grasslands has been
27 the focus of an increasing number of studies in recent years, likely in response to increas-
28 ingly visible vegetation and landscape changes in ecosystems where this process takes
29 place.² This process of encroachment generally involves **increases in number and/or**
30 **density**³ of woody shrub-like plants in a given area (Van Auken, 2000), which can dis-
31 place other species and **alter the local ecosystem**⁴. Woody plant encroachment has been
32 observed across many arid and semi-arid regions, such as the grasslands of the southwest-
33 ern United States (Van Auken, 2000, 2009; Goslee et al., 2003; Gibbens et al., 2005) and
34 southern South America (Parizek et al., 2002; Cabral et al., 2003), savannas of southern
35 Africa (Trollope et al., 1989; Roques et al., 2001), and Asian steppes (Peng et al., 2013;
36 Chen et al., 2015). These shrub **invasions**⁵ are often regarded as **ecological issues**⁶ in the
37 places where they occur, with the increasing shrub biomass and dispersal being consid-
38 ered as strong drivers of ecosystem degradation and/or desertification (Schlesinger et al.,
39 1990; Ravi et al., 2009) due to how these plants alter the distribution of soil resources
40 (Schlesinger and Pilmanis, 1998; Knapp et al., 2008). In other places, ecosystem function
41 and dynamics may be altered **in ways that are significantly different**⁷ and depend on the
42 traits of the invading shrubs (Eldridge et al., 2011). Other adverse effects of encroach-
43 ment include changes in ecosystem services (Reed et al., 2015; Kelleway et al., 2017),
44 declines in biodiversity (Ratajczak et al., 2012; Sirami and Monadjem, 2012; Brandt
45 et al., 2013), and economic losses in areas where the proliferation of shrubs adversely

²*I think this opening sentence can be stronger. The fact that a lot of studies focus on encroachment is not what makes it interesting. The second clause does not really say anything.*

³*this description misses the spatial aspect*

⁴*vague*

⁵*I would either avoid this word or be explicit about how you use it. Many ecologists associate 'invasion' with exotic plants. I think it is worth pointing out that shrub encroachment often involves native plants.*

⁶*vague*

⁷*Vague. This sentence does not say much. I would make it say more or delete.*

46 affects grazing land and pastoral production (Mugasi et al., 2000; Oba et al., 2000).⁸

47 The encroachment of woody plants into adjacent grasslands involves the movement
48 of shrub-grass ecotones, and this kind of expansion can be modelled⁹ as a propagating
49 wave that is a gradient of conspecific density varying in both space and time (Kot et al.,
50 1996; Neubert and Caswell, 2000; Wang et al., 2002; Pan and Lin, 2012). The movement
51 of these waves is dependent upon two processes: dispersal of propagules and local de-
52 mography. First¹⁰, movement is driven by the spatial dispersal of propagules produced
53 by parent plants. The speed at which expansion waves move is highly dependent upon
54 the dispersal kernel¹¹ shape, especially regarding the frequency of long-distance dispersal
55 events at the tail of the distribution (Skares and Shea, 2007). Second¹², while dispersal
56 plays a role in where the new recruits that drive the wave's movement are likely to be
57 found, demographic processes are important as well since survival, growth, reproduction,
58 and recruitment rates in the parent plant ultimately affect the number of propagules
59 produced and their fate after release. These demographic processes can strongly affect
60 how waves move, and structured populations in which rates vary between age, size, or
61 life stage can be sensitive to demographic changes that may alter patterns of expansion¹³
62 (Neubert and Caswell, 2000).

63 Given that expansion waves typically correspond to gradients of conspecific density,
64 the effects of density dependence on demographic rates and population growth are im-
65 portant to consider.¹⁴ Not¹⁵ only does the density of plants influence the strength of

⁸ *I think it would be good for this first paragraph to introduce the idea of habitat ecotones, the need to understand whether these are stable, and how they may respond to global change drivers. You can then introduce woody encroachment as a specific and widespread type of ecotone.*

⁹ *Modeling is a method. It is not very meaningful to say ecotones can be 'modeled' without first saying what it is we want to understand about them. Keep the focus here on the conceptual problems.*

¹⁰ *Might be more intuitive to start with demography.*

¹¹ *You have not introduced or defined 'dispersal kernel', so many readers will not know what you mean by its 'shape'.*

¹² *This sentence could be stronger and more informative*

¹³ *Unclear what you mean or why this would be unique to structured populations. I think this paragraph should more clearly explain the importance of population structure in both demography and dispersal. This sets up the idea that seed dispersal may depend on plant size.*

¹⁴ *This is a good topic sentence. It is clear where the paragraph is going from here.*

¹⁵ *This sentence is hard to read and has awkward grammar. Try re-writing.*

66 resource competition amongst them and thus the extent to which they survive, grow and
 67 reproduce, but it also can determine whether a dispersed propagule will germinate and
 68 grow or if its competitors will prevent it from becoming established. Since intraspecific
 69 competition governs the performance of individuals within the population, **the part of the**
 70 **population responsible for wave movement**¹⁶ is strongly tied to how demographic rates
 71 and population growth vary with changes in conspecific density. If population growth has
 72 a negative and monotonic relationship with density such that highest **rates of growth**¹⁷
 73 tend to be found at the lowest densities, then the invading wave is pulled forward by
 74 the plants at the low-density vanguard (Kot et al., 1996). However, **if Allee effects result**
 75 **in reduced fitness at low densities**¹⁸, then the wave is instead pushed forward by the
 76 individuals behind the front edge (Kot et al., 1996; Taylor and Hastings, 2005; Sullivan
 77 et al., 2017). Such Allee effects can greatly limit population growth at the front of the
 78 wave, **slowing**¹⁹ or halting its movement (Lewis and Kareiva, 1993; Veit and Lewis, 1996;
 79 Keitt et al., 2001).

80 20

81 Ecological theory for invasion waves as described above provides a tool that can be
 82 used to better **understand**²¹ and manage woody encroachment, **with many sites of shrub**
 83 **expansion around the world providing opportunities to do so**²². **One particular site of**
 84 **interest**²³ is the Chihuahuan Desert of the southwestern United States, where **extensive**

¹⁶ *Unclear what you mean by this*

¹⁷ *Unclear whether you mean individual growth or population growth*

¹⁸ *I think this needs to be unpacked a bit more, explaining why fitness may be reduced at low density.*

¹⁹ *I think it would help to have a more explicit statement that, all else equal, a pushed wave should be slower than a pulled wave – I think this is true but we should check and cite, obviously. See two nice references that I will email.*

²⁰ *I think there should be a new paragraph here that connects the pulled/pushed ideas to shrub encroachment. There is a lot of literature on woody plants being ecosystem engineers. While these are not typically called ‘Allee effects’, you can make the link that we might expect positive density dependence at the leading edge of woody ecotones, and this could slow or halt their expansion. I think this will be an important addition for building your story.*

²¹ *It is still not explicit from your writing what it is we need to understand about encroachment. This will be helpful to add.*

²² *Very little information here.*

²³ *I think this is an awkward transition. Would be better to start a new paragraph with ‘In this study,*

documentation of shrub encroachment already exists²⁴. Here, populations of the creosote-bush (*Larrea tridentata*) have been expanding into nearby grasslands for approximately 150 years and have decreased the cover of grasses such as *Bouteloua eriopoda* (Gardner, 1951; Buffington and Herbel, 1965; Gibbens et al., 2005). This encroachment leads to ecotones marking a transition from dense shrubland with numerous dry patches to open grassland, with a transition zone in between where larger²⁵ shrubs can often be found interspersed among their grassy competitors.²⁶ Historically, long-term creosotebush encroachment into grasslands is believed to have been driven by a combination of factors including overgrazing, drought and 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 feedback (Grover and Musick, 1990; D’Odorico et al., 2012) by modifying various aspects of their surroundings²⁷ that could favour continued growth and dispersal²⁸, such as local climate (D’Odorico et al., 2010) and rates of soil erosion (Turnbull et al., 2010). Such positive feedback also occurs as herbaceous competitors are eliminated, reducing competition as well as the amount of flammable biomass used to fuel the fires that keep creosotebush growth in check (Van Auken, 2000).

In²⁹ addition to these large-scale observations of encroachment, some demographic data on creosotebush are also present and may prove useful in connecting encroachment observations to mathematical models of propagating population wave fronts. Several studies have shown a negative relationship between size and conspecific density in *Larrea*

we...’ and then jump into the SEV system. You can then go on to describe (as you do below) why this is a compelling system for questions about encroachment.

²⁴*This obscures the novel contribution of this study. I would rephrase this.*

²⁵*This is hinting at results, so maybe not the place for it.*

²⁶*We might consider including a photo, depending on the journal. Ecology publishes photos as part of articles.*

²⁷*vague*

²⁸*Again, I would connect this back to Allee effects/pushed waves, since it suggests that seeds that recruit into high grass densities at the leading edge should suffer from lack of conspecifics.*

²⁹*I think this paragraph could be reduced or eliminated. None of the previous studies give us the information we need to infer wave speed. You could just say in the previous paragraph that while there is a lot of interest in creosote expansion, no previous studies have evaluated demography and dispersal to understand and predict expansion dynamics.*

105 tridentata (Yeaton et al., 1977; Phillips and MacMahon, 1981; Miller and Huenneke,
106 2000), indicating that density dependence likely regulates resource intake and controls
107 growth in competing shrubs. There is also evidence for a negative relationship between
108 number of fruits and conspecific density (Miller and Huenneke, 2000), suggesting that
109 creosotebush fecundity is higher in areas with fewer conspecific neighbours. Overall
110 though, the amount of literature investigating density dependence of demographic rates
111 and population growth in creosotebush is still rather limited. There is also relatively little
112 understanding of how density-dependent demography and population growth facilitate
113 creosotebush expansion, as well as a dearth of data regarding population dynamics at the
114 vanguard of expanding creosotebush populations. Without better knowledge on all of
115 these, it becomes rather difficult to mathematically model creosotebush encroachment, as
116 doing so requires knowledge of the mechanisms occurring at these grass-shrub boundaries.
117 Such gaps in knowledge make it difficult to make estimates of encroachment rates that
118 extend beyond what can be gathered from vegetation surveys.

119 This research aims to fill these knowledge gaps **by not only collecting better data on**
120 **demographic rates**³⁰ and dispersal in *Larrea tridentata*, but also by **connecting it to the**
121 **mathematical models that portray encroaching populations as propagating waves through**
122 **space and time.** These investigations are novel in the sense that they will be some of the
123 first to apply the aforementioned mathematical model to ecotones of *Larrea tridentata*
124 and its grassy competitors, using density-dependent demographic rates and recruitment
125 to describe the dynamics of ecotone movement in this specific system.³¹ First, we quantify
126 how demographic rates such as survival, annual growth, and reproduction vary across
127 both the distribution of shrub sizes as well as a gradient of conspecific density. These
128 demographic data allow us to analyse the pattern of density dependence to see whether
129 this density dependence is strictly monotonic and population growth is maximised at the

³⁰ *I would not both calling it 'better', following my comment above.*

³¹ *All of this text emphasizes the mathematical modeling without framing the question(s) that the model is meant to answer.*

lowest conspecific density or if Allee effects are present. This will also let us understand if the invasion wave is pulled by the individuals at the front or instead pushed by the individuals behind it. Second, we use a fluid dynamics model to investigate wind dispersal capabilities in this species and construct dispersal kernels to estimate the probability of propagules travelling a given distance. Finally, we combine our data on demographic rates and dispersal, using a spatial integral projection model to obtain estimates for the approximate speed at which the wave advances.³²

Materials and methods

Study system

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 conducted in summer 2001 and again in summer 2013 to document change in the spatial extent of shrub encroachment. 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 analysis, we visually assessed midpoint values of these cover classes at each meter location for both transects and years.

³²*I suggest re-writing this as a numbered list of either questions or objectives (I think questions is generally better but both could work). These could then be used to structure the methods and results. These sections are in need of greater structure.*

147 **Demographic data collection**

148 **Observational surveys**

149 **Transplant experiment**

150 **Demographic data analysis**

151 **Observational surveys**

152 **Transplant experiment**

153 Collection of creosotebush demographic data occurred during the early summer of every
154 year from 2013-2017, at the Sevilleta National Wildlife Refuge LTER site in central New
155 Mexico. Four different sampling sites in the eastern part of the reserve were designated,
156 with each of the sites containing 3 different transects. Lengths of these transects varied
157 from 200 to 600 m, and no two sites had identical compositions of transect lengths.
158 Transect length was determined by the strength of vegetation transition, as areas where
159 shrubland more quickly transitions to grassland do not need as long of a transect to
160 capture the gradient of densities as a more gradual transition does. All transects were
161 placed longitudinally along the shrubland-grassland ecotone so a full range of shrub
162 densities could be captured; each transect spanned shrub-dense "core" areas as well as
163 grasslands with few shrubs and the transition zones in between.

164 Only plants within a metre of the transect on either side were considered when de-
165 termining baseline shrub densities. These densities were calculated using initial mea-
166 surements from 2013 and were assumed to remain relatively static over the course of
167 the study; each density was recorded as the weighted total amount of shrub volume per
168 5-m transect subsection. The per-shrub volume was calculated as that of an elliptic
169 cone, as this was found to be the figure most closely matching the plant's morphology,
170 using the formula $V_i = \pi lwh/3$ where l , w , and h are the maximum length, maximum
171 width, and height, respectively. Maximum length and width were measured so that they

172 were always perpendicular to each other, and height was measured from the base of
173 the woody stem at the soil surface to the highest part of the shrub. All three of these
174 dimensional measurements were mutually orthogonal and were inclusive only of living
175 parts of the shrub; dead wood and non-foliated outer sections were not included in mea-
176 surements. The total weighted density for the window was then expressed as the sum
177 of log-transformed volumes of each individual shrub contained within. Such a weighted
178 density was chosen because density of individuals alone can often fail to be a useful mea-
179 surement in environments where large size differences between plants of the same species
180 exist. Different-sized plants may vary greatly in their ability to extract resources from the
181 environment around them and may thus differ greatly in their degree of competitiveness
182 (Weiner, 1990; HARA, 1993). By using a weighted density in terms of shrub volume,
183 we were able to account for the extra competitiveness of larger shrubs and thus have
184 a more accurate measurement of conspecific presence that is more suitable for a study
185 population containing significant heterogeneity in size.

186 A subset of the shrubs used to calculate the baseline densities were tagged, with each
187 plant given a unique identifier that allowed it to be recognised based on sampling site,
188 transect number, and location within 50-m and 5-m subsections. These tagged shrubs
189 then had various demographic measurements recorded on an annual basis. Maximum
190 width, length, and height on each shrub were measured in order to calculate conical
191 volume, using the formula given earlier. Survival status of the shrubs was also recorded,
192 with dead individuals being noted and excluded from measurements in subsequent years.
193 Counts of flowers and fruits on each shrub were recorded as well. In instances where
194 shrubs had large numbers of reproductive structures that would prove difficult to reliably
195 count, estimates were made, with a more accurate count on a fraction of the shrub being
196 extrapolated to the entire individual. The position of each shrub along the transect was
197 noted to a resolution of 5 m so that it could be matched with the baseline density of its
198 corresponding subsection. For shrubs in which a given 5-m subsection was not recorded,

their position was estimated to the nearest 50 m; however, compared to the number of finer-resolution 5-m subsections, this occurred relatively infrequently. Establishment of recruits was also accounted for, with new recruits observed within the study area tagged and measured.

Collected demography data were then examined to investigate how weighted density and shrub volume affected four different demographic variables: survival, probability of flowering (i.e. producing at least one flower or fruit), annual growth, and number of reproductive structures. Each of these demographic variables was fit to a different mixed-effects model through maximum likelihood. Both survival and probability of flowering were each fit to generalised linear mixed-effects models using a binomial response and a logit link function. Annual growth was defined as $\ln(V_{t+1}/V_t)$ where V_{t+1} and V_t are the shrub volumes in the current and previous years, respectively, and was then fit to a linear mixed-effects model. The number of reproductive structures was defined as the natural logarithm of the sum of fruits and flowers on the entire shrub and was fit to a linear mixed-effects model as well. To construct these models, all of the equations listed in Table 1 were first fit to each of the four demographic variables, with each equation using volume and standardised density as predictors while also treating the unique transect in which each shrub was located as a random effect. After these equations were fit to the data, all eight equations for each demographic variable were ranked based on their value of the Akaike information criterion (AIC) and weighted based on their quality so that better-fitting models had a higher weight. Then, coefficients of the same type were averaged between all eight models for each demographic variable using a weighted mean corresponding to model quality in order to generate an average model. All four average models have the general form

$$R = \beta_1 v + \beta_2 d + \beta_3 d^2 + \beta_4 v d + \beta_5 v d^2 + \epsilon \quad (1)$$

where R is the response variable, v and d are the volume and density, ϵ is a random transect effect, and β is the coefficient for each type of term.

The effect of density dependence on the probability of recruitment from seeds was also modelled. For every year, the sum of seeds produced the prior year was calculated for each 5-m subsection, and then probability of recruitment was calculated as the number of recruits observed in each 5-m subsection divided by that number of seeds. For any subsection in which seeds were not found, a count of seeds was estimated based on the number of seeds in a subsection of similar weighted density; this was done to avoid creating any undefined values of recruitment probability. Both linear and quadratic models using only weighted density as a predictor were fit to the distribution of recruitment probabilities, though the linear model was ultimately used because it had a higher AIC value.

Seed dispersal

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

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

that is a slight adaptation from equation 5b in Katul et al. (2005), using r to denote

249 dispersal distance. Here, λ' is the location parameter and μ' is the scale parameter,
 250 which depend on environmental and plant-specific properties of the study system. The
 251 location and scale parameters are defined as $\lambda' = (H/\sigma)^2$ and $\mu' = HU/F$; these are
 252 functions of the height H of seed release, wind speed U at seed release height, seed
 253 terminal velocity F , and the turbulent flow parameter σ that depends on both wind
 254 speed and local vegetation roughness.

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

$$258 \quad U = \frac{1}{H} \int_{d+z_0}^H \frac{u^*}{K} \log \left(\frac{z-d}{z_0} \right) dz \quad (3)$$

259 given in Bullock et al. (2012) equation 6, with the notation slightly modified. Here, z
 260 is the height above the ground, K is the von Karman constant, and u^* is the friction
 261 velocity. The zero-plane displacement d and roughness length z_0 are surface roughness
 262 parameters that, for a grass canopy height h above the ground, are approximated by
 263 $d \approx 0.7h$ and $z_0 \approx 0.1h$. These estimates are from Raupach (1994) for a canopy area
 264 index $\Lambda = 1$ in which the sum of grass canopy elements is equal to the unit area being
 265 measured. A 0.15 m grass height at the study site gives $d = 0.105$ and z_0 , which are
 266 suitable approximations for grassland (Wiernga, 1993). Calculations of u^* were done
 267 using equation A2 from Skarpaas and Shea (2007), in which

$$268 \quad u^* = KU_m \left[\log \left(\frac{z_m - d}{z_0} \right) \right]^{-1} \quad (4)$$

269 and U_m is the mean wind velocity at the measurement height z_m . Values for the turbulent
 270 flow parameter σ were then calculated using the estimate made by Skarpaas and Shea

271 (2007) in their equation A4, where

$$272 \quad \sigma = 2A_w^2 \sqrt{\frac{K(z-d)u^*}{C_0 U}} \quad (5)$$

273 and C_0 is the Kolmogorov constant. A_w is a constant that relates vertical turbulence
 274 to friction velocity and is approximately equal to 1.3 under the assumptions of above-
 275 canopy flow made by Skarpaas and Shea (2007), based off calculations from Hsieh and
 276 Katul (2005). In addition, the assumption that $z = H$ was made in order to make the
 277 calculation of σ more feasible.

278 The values from the previous three equations give us the necessary information to
 279 calculate μ' and λ' , thus allowing us to create the WALD distribution $p(r)$. However, the
 280 base WALD model does not take into account variation in wind speeds or seed terminal
 281 velocities, which limits its applicability in systems where such variation is present. In
 282 order to account for this variation, we integrate the WALD model over distributions these
 283 two variables using the same method as Skarpaas and Shea (2007). The WALD model
 284 assumes seed release from a single point source, though, which is not realistic for a shrub;
 285 because seeds are released across the entire height of the shrub rather than from a point
 286 source, $p(r)$ was also integrated across the uniform distribution from the grass canopy
 287 height to the shrub height. Thus, under the assumptions that the height at which a
 288 seed is located does not affect its probability of being released and that seeds are evenly
 289 distributed throughout the shrub, this gives the dispersal kernel $K(r)$, where

$$290 \quad K(r) = \iiint p(F)p(U)p(z)p(r) dF dU dz \quad (6)$$

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

293 The distribution $p(F)$ in the integral above was constructed using experimentally
 294 determined seed terminal velocities. This was done by using a high-speed camera and

295 motion tracking software to determine position as a function of time, and then using the
 296 Levenberg-Marquardt algorithm to solve a quadratic-drag equation of motion for F . Be-
 297 fore seeds were released, they were dried and then dyed with yellow fluorescent powder,
 298 and then put against a black background to improve visibility and make tracking easier.
 299 While the powder added mass to the seeds, this added mass only yielded an approxi-
 300 mately 2.5% increase and was thus negligible, likely having little effect on their terminal
 301 velocities. Measurements were conducted for 48 seeds that were randomly chosen from a
 302 seed pool derived from different plants, and then an empirical PDF of terminal velocities
 303 was constructed using the data. Constructing $p(U)$ involved creating an empirical PDF
 304 of hourly wind speeds at Five Points, the site closest to the 12 transects being used,
 305 that were obtained from meteorological data collected at the Seville National Wildlife
 306 Refuge from 1988 to 2010. We did not weight $p(U)$ and assumed that the probability
 307 seed release from the shrub is the same regardless of wind speed.

308 *Wave model using spatial integral projection models*

309 Given that the shrub population at this site is approximately homogeneous perpen-
 310 dicular to the direction of encroachment, expansion is modelled as a wave moving in one
 311 dimension. A spatial integral projection model (SIPM) is used to estimate the speed at
 312 which encroachment occurs; such a model incorporates the effects of variation in traits
 313 like plant size that stage-structured models, such as those described in Neubert and
 314 Caswell (2000), do not capture. According to Jonjégans et al. (2011), a general SIPM
 315 can be formulated as

$$316 \quad \mathbf{n}(x_2, z_2, t + 1) = \iint \tilde{K}(x_2, x_1, z_2, z_1) \mathbf{n}(x_1, z_1, t) dx_1 dz_1 \quad (7)$$

317 where x_1 and x_2 are locations of individuals of a particular size before and after one unit of
 318 time, and z_1 and z_2 are the respective sizes. The vector \mathbf{n} indicates the population density
 319 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 Jonjégans et al. (2011). Here,

$$\tilde{K}(x_2, x_1, z_2, z_1) = K(x_2 - x_1)Q(z_2 - z_1) + \delta(x_2 - x_1)G(z_2 - z_1) \quad (8)$$

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

$$c^* = \min_{s>0} \left[\frac{1}{s} \ln(\rho_s) \right] \quad (9)$$

where s is the wave shape parameter and ρ_s is the dominant eigenvalue of the kernel \mathbf{H}_s (Jonjégans 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

$$\mathbf{H}_s = M(s)Q(z_2 - z_1) + G(z_2 - z_1) \quad (10)$$

345 where $M(s)$ is the moment-generating function of the dispersal kernel (Jongejans et al.,
 346 2011). For one-dimensional dispersal, this moment-generating function can be estimated
 347 as

$$348 \quad M(s) = \frac{1}{N} \sum_{i=1}^n I_0(sr_i) \quad (11)$$

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

357 **Results**

358 **Encroachment re-surveys**

359 Figure 1.

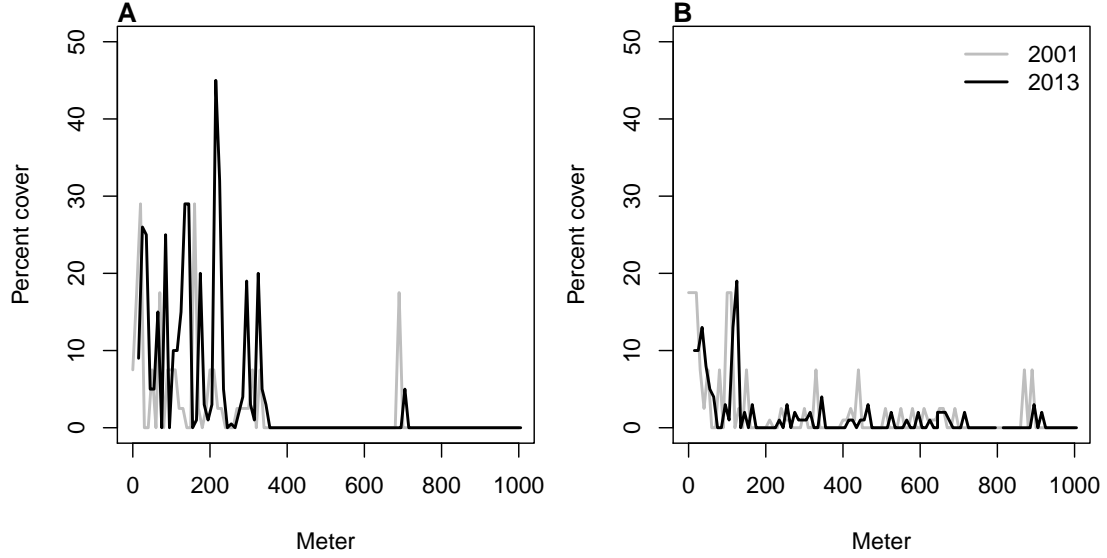


Figure 1: Re-surveys of shrub cover along two permanent trasects (A,B) surveyed in 2001 and 2013.

360 The speed of encroachment at the study site as estimated by the SIPM is rather
 361 slow; as can be seen in Figure 2, the low-density wavefront moves at approximately
 362 0.5 cm/yr under normal conditions and at 1 cm/yr under the best seedling survival
 363 conditions observed in the dataset. These improved conditions were observed due to
 364 above-average rainfall that occurred after greenhouse-grown seedlings were transplanted
 365 to the site. Population growth in this low-density region of the moving wave is also low,
 366 with a geometric growth rate of $\lambda \approx 1.006$ and even lower rates of growth the higher-
 367 density regions behind; in the higher-survival scenario the maximum rate increases to
 368 $\lambda \approx 1.013$, with growth still decreasing as density increases. For both scenarios, the
 369 decrease in population growth rate with increasing density was monotonic across the
 370 range of observed standardised densities, as is shown in Figure 2. This suggests that
 371 an Allee effect is likely not present in this population, as the highest rate of population
 372 growth is found at the lowest density vanguard of the encroaching population. Thus, the
 373 conditions necessary for equation 9 to be valid are satisfied, and these wavespeeds are
 374 applicable for a pulled-wave scenario in which no Allee effects are present.

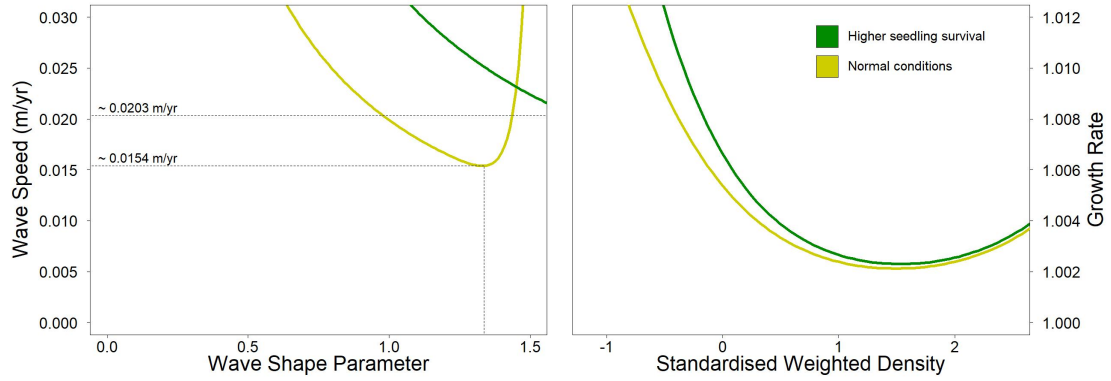


Figure 2: Estimated encroachment wave speeds (left) and geometric rates of population growth (right) for higher post-rainfall seedling survival and normal conditions.

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 3 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

392 $K(r)$ varies greatly among the shrub population given the large range of shrub heights
 393 observed; shrubs at lower heights have more slender kernels with most of the seeds dis-
 394 persing closer to the plant, while taller shrubs have kernels with much fatter tails and
 395 are more capable of longer-distance dispersal.

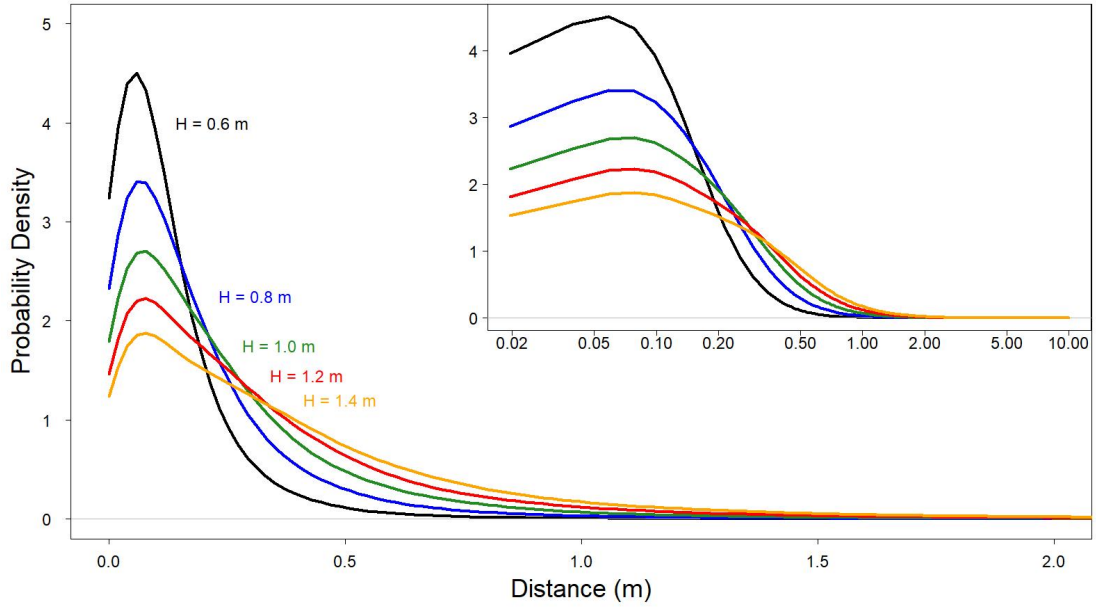


Figure 3: Dispersal kernels, with each colour representing a selected shrub height. The inset plot is the same as the large plot, though with a logarithmic x-axis to more easily show differences in dispersal probability at smaller distances.

396 Density and size dependence are evident in all 4 of the demographic rates, with
 397 coefficients for each model displayed in Table 2. For growth, reproduction, and survival,
 398 density dependence is mostly negative and monotonic; this is not the case for probability
 399 of flowering, where shrub size seems to be more important than the effects of density alone
 400 and suggests that larger shrubs have a higher probability of flowering than their smaller
 401 counterparts. This, along with size and density dependence in growth and reproduction,
 402 is shown in Figure 4. Size dependence is positive for reproduction, as would be expected
 403 since larger plants typically produce more flowers and fruits. However, annual growth

404 decreases as size increases; this could be in part due to the annual growth in this study
405 being quantified as a proportion relative to the shrub's initial size. While larger shrubs
406 may produce more plant material over a year in terms of absolute volume, smaller shrubs
407 produce less but can still have higher annual growth in terms of the percentage of volume
408 added relative to their initial volume. When compared to density, shrub size is a much
409 stronger predictor of survival, with significant differences in mortality rates depending on
410 shrub size. For small shrubs, mortality is exceptionally high, and increases in volume for
411 these shrubs only slightly increase the likelihood of survival. However, after shrubs reach
412 a logarithmic volume of approximately 7.3, they are almost guaranteed to survive, with
413 survival rates near 100% persisting regardless of any further size increases. Interestingly,
414 though most recruits were found at lower densities, the probability of recruitment from
415 seed displays positive density dependence; the probability of recruitment was still very
416 low, though, with a baseline rate of approximately 2 recruits per 10,000 seeds.

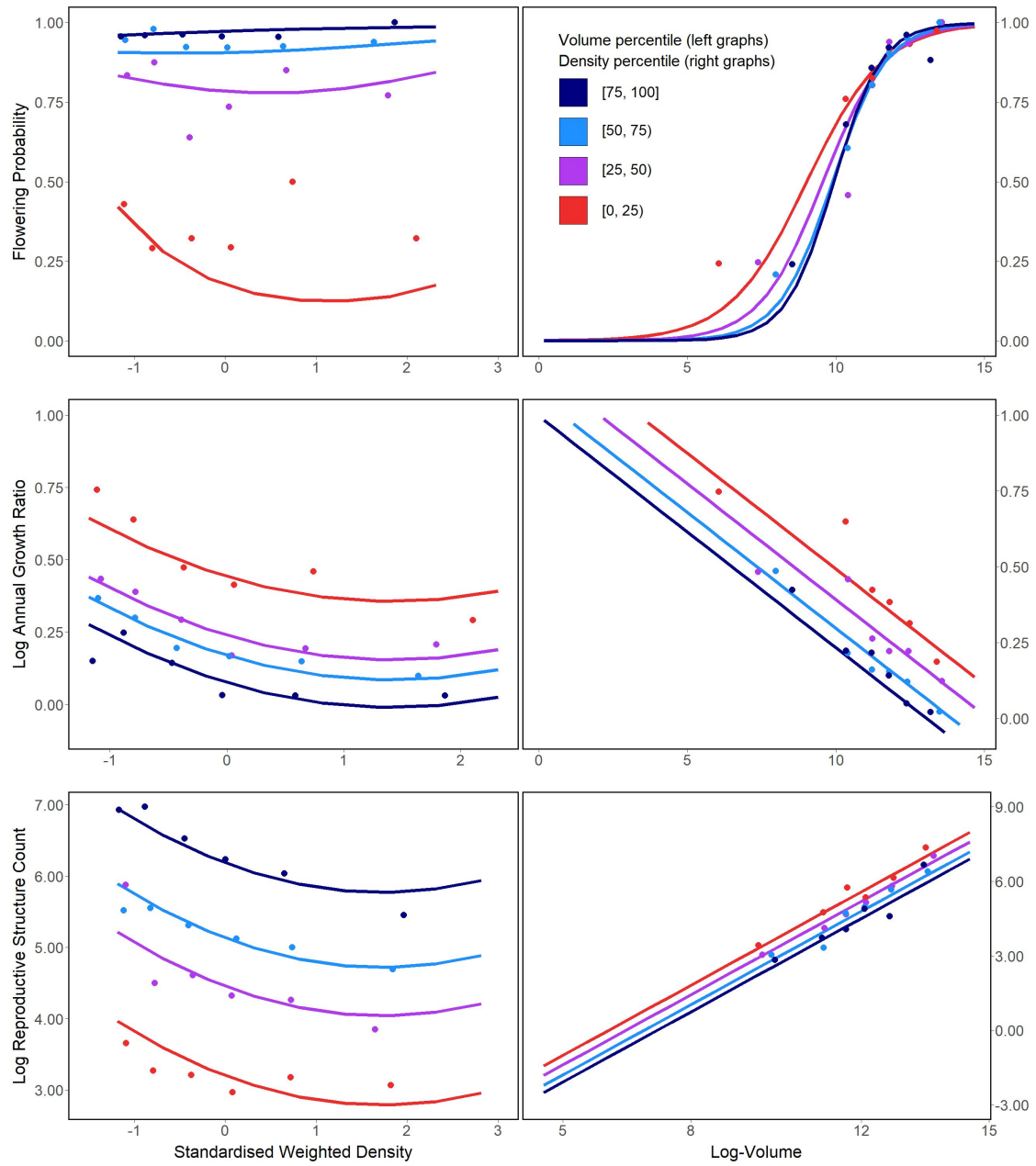


Figure 4: Flowering probability (top row), log annual growth ratio (centre row), and log reproductive structure count (bottom row) at all four sampling sites. In the left column of graphs, the three response variables are shown as a function of density for each of four volume quartiles, with each quartile 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

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

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

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

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

493 Acknowledgements

494 Author contributions

495 Data accessibility

496 References

- 497 Bowers, J. E., R. M. Turner, and T. L. Burgess. 2004. Temporal and spatial patterns in
498 emergence and early survival of perennial plants in the Sonoran Desert. *Plant Ecology*
499 **172**:107–119.
- 500 Boyd, R. S., and G. D. Brum. 1983. Postdispersal reproductive biology of a Mojave Desert
501 population of *Larrea tridentata* (Zygophyllaceae). *American Midland Naturalist* pages
502 25–36.
- 503 Brandt, J. S., M. A. Haynes, T. Kuemmerle, D. M. Waller, and V. C. Radeloff. 2013.
504 Regime shift on the roof of the world: Alpine meadows converting to shrublands in
505 the southern Himalayas. *Biological Conservation* **158**:116–127.
- 506 Buffington, L. C., and C. H. Herbel. 1965. Vegetational changes on a semidesert grassland
507 range from 1858 to 1963. *Ecological monographs* **35**:139–164.
- 508 Cabral, A., J. De Miguel, A. Rescia, M. Schmitz, and F. Pineda. 2003. Shrub encroach-
509 ment in Argentinean savannas. *Journal of Vegetation Science* **14**:145–152.
- 510 Chen, L., H. Li, P. Zhang, X. Zhao, L. Zhou, T. Liu, H. Hu, Y. Bai, H. Shen, and J. Fang.
511 2015. Climate and native grassland vegetation as drivers of the community structures
512 of shrub-encroached grasslands in Inner Mongolia, China. *Landscape Ecology* **30**:1627–
513 1641.

- 514 Chew, R. M., and A. E. Chew. 1970. Energy relationships of the mammals of a desert
515 shrub (*Larrea tridentata*) community. *Ecological Monographs* pages 2–21.
- 516 D’Odorico, P., J. D. Fuentes, W. T. Pockman, S. L. Collins, Y. He, J. S. Medeiros,
517 S. DeWekker, and M. E. Litvak. 2010. Positive feedback between microclimate and
518 shrub encroachment in the northern Chihuahuan desert. *Ecosphere* **1**:1–11.
- 519 D’Odorico, P., G. S. Okin, and B. T. Bestelmeyer. 2012. A synthetic review of feedbacks
520 and drivers of shrub encroachment in arid grasslands. *Ecohydrology* **5**:520–530.
- 521 Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whit-
522 ford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning:
523 towards a global synthesis. *Ecology letters* **14**:709–722.
- 524 Gardner, J. L. 1951. Vegetation of the creosotebush area of the Rio Grande Valley in
525 New Mexico. *Ecological Monographs* **21**:379–403.
- 526 Gibbens, R., R. McNeely, K. Havstad, R. Beck, and B. Nolen. 2005. Vegetation changes
527 in the Jornada Basin from 1858 to 1998. *Journal of Arid Environments* **61**:651–668.
- 528 Goslee, S., K. Havstad, D. Peters, A. Rango, and W. Schlesinger. 2003. High-resolution
529 images reveal rate and pattern of shrub encroachment over six decades in New Mexico,
530 USA. *Journal of Arid Environments* **54**:755–767.
- 531 Grover, H. D., and H. B. Musick. 1990. Shrubland encroachment in southern New Mexico,
532 USA: an analysis of desertification processes in the American Southwest. *Climatic*
533 *change* **17**:305–330.
- 534 HARA, T. 1993. Mode of competition and size-structure dynamics in plant communities.
535 *Plant Species Biology* **8**:75–84.
- 536 Jongejans, E., K. Shea, O. Skarpaas, D. Kelly, and S. P. Ellner. 2011. Importance of

individual and environmental variation for invasive species spread: a spatial integral
projection model. *Ecology* **92**:86–97.

Katul, G., A. Porporato, R. Nathan, M. Siqueira, M. Soons, D. Poggi, H. Horn, and
S. A. Levin. 2005. Mechanistic analytical models for long-distance seed dispersal by
wind. *The American Naturalist* **166**:368–381.

Keitt, T. H., M. A. Lewis, and R. D. Holt. 2001. Allee effects, invasion pinning, and
species’ borders. *The American Naturalist* **157**:203–216.

Kelleway, J. J., K. Cavanaugh, K. Rogers, I. C. Feller, E. Ens, C. Doughty, and N. Sain-
tilan. 2017. Review of the ecosystem service implications of mangrove encroachment
into salt marshes. *Global Change Biology* **23**:3967–3983.

Knapp, A. K., J. M. Briggs, S. L. Collins, S. R. Archer, M. S. BRET-HARTE, B. E.
Ewers, D. P. Peters, D. R. Young, G. R. Shaver, E. Pendall, et al. 2008. Shrub
encroachment in North American grasslands: shifts in growth form dominance rapidly
alters control of ecosystem carbon inputs. *Global Change Biology* **14**:615–623.

Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of
invading organisms. *Ecology* **77**:2027–2042.

Lei, S. A. 1999. Ecological impacts of *Pogonomyrmex* on woody vegetation of a *Larrea*-
Ambrosia shrubland. *The Great Basin Naturalist* pages 281–284.

Lewis, M., and P. Kareiva. 1993. Allee dynamics and the spread of invading organisms.
Theoretical Population Biology **43**:141–158.

Lewis, M. A., M. G. Neubert, H. Caswell, J. S. Clark, and K. Shea, 2006. A guide
to calculating discrete-time invasion rates from data. Pages 169–192 *in* *Conceptual
ecology and invasion biology: reciprocal approaches to nature*. Springer.

- 560 Miller, R. E., and L. F. Huenneke. 2000. The relationship between density and demo-
561 graphic variation within a population of *Larrea tridentata*. *The Southwestern Natu-*
562 *ralist* pages 313–321.
- 563 Moreno-de las Heras, M., L. Turnbull, and J. Wainwright. 2016. Seed-bank structure
564 and plant-recruitment conditions regulate the dynamics of a grassland-shrubland Chi-
565 huahuan ecotone. *Ecology* **97**:2303–2318.
- 566 Mugasi, S., E. Sabiiti, and B. Tayebwa. 2000. The economic implications of bush
567 encroachment on livestock farming in rangelands of Uganda. *African Journal of Range*
568 *and Forage Science* **17**:64–69.
- 569 Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: calculation and
570 sensitivity analysis of invasion speed for structured populations. *Ecology* **81**:1613–
571 1628.
- 572 Oba, G., E. Post, P. Syvertsen, and N. Stenseth. 2000. Bush cover and range condition
573 assessments in relation to landscape and grazing in southern Ethiopia. *Landscape*
574 *ecology* **15**:535–546.
- 575 Pan, S., and G. Lin. 2012. Invasion traveling wave solutions of a competitive system
576 with dispersal. *Boundary Value Problems* **2012**:120.
- 577 Parizek, B., C. M. Rostagno, and R. Sottini. 2002. Soil erosion as affected by shrub
578 encroachment in northeastern Patagonia. *Rangeland Ecology & Management/Journal*
579 *of Range Management Archives* **55**:43–48.
- 580 Peng, H.-Y., X.-Y. Li, G.-Y. Li, Z.-H. Zhang, S.-Y. Zhang, L. Li, G.-Q. Zhao, Z.-Y. Jiang,
581 and Y.-J. Ma. 2013. Shrub encroachment with increasing anthropogenic disturbance
582 in the semiarid Inner Mongolian grasslands of China. *Catena* **109**:39–48.

583 Phillips, D. L., and J. A. MacMahon. 1981. Competition and spacing patterns in desert
584 shrubs. *The Journal of Ecology* pages 97–115.

585 Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. Woody encroachment decreases
586 diversity across North American grasslands and savannas. *Ecology* **93**:697–703.

587 Ravi, S., P. D’Odorico, S. L. Collins, and T. E. Huxman. 2009. Can biological invasions
588 induce desertification? *The New Phytologist* **181**:512–515.

589 Reed, M., L. Stringer, A. Dougill, J. Perkins, J. Athopheng, K. Mulale, and N. Favretto.
590 2015. Reorienting land degradation towards sustainable land management: Linking
591 sustainable livelihoods with ecosystem services in rangeland systems. *Journal of envi-
592 ronmental management* **151**:472–485.

593 Roques, K., T. O’connor, and A. R. Watkinson. 2001. Dynamics of shrub encroach-
594 ment in an African savanna: relative influences of fire, herbivory, rainfall and density
595 dependence. *Journal of Applied Ecology* **38**:268–280.

596 Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant-soil interactions in deserts. *Biogeo-
597 chemistry* **42**:169–187.

598 Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell,
599 R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification.
600 *Science* **247**:1043–1048.

601 Sirami, C., and A. Monadjem. 2012. Changes in bird communities in Swaziland savannas
602 between 1998 and 2008 owing to shrub encroachment. *Diversity and Distributions*
603 **18**:390–400.

604 Skarpaas, O., and K. Shea. 2007. Dispersal patterns, dispersal mechanisms, and invasion
605 wave speeds for invasive thistles. *The American Naturalist* **170**:421–430.

606 Sullivan, L. L., B. Li, T. E. Miller, M. G. Neubert, and A. K. Shaw. 2017. Density depen-
607 dence in demography and dispersal generates fluctuating invasion speeds. *Proceedings*
608 of the National Academy of Sciences **114**:5053–5058.

609 Taylor, C. M., and A. Hastings. 2005. Allee effects in biological invasions. *Ecology*
610 Letters **8**:895–908.

611 Thompson, S. E., S. Assouline, L. Chen, A. Trahktenbrot, T. Svoray, and G. G. Katul.
612 2014. Secondary dispersal driven by overland flow in drylands: Review and mechanistic
613 model development. *Movement ecology* **2**:7.

614 Trollope, W., F. Hobson, J. Danckwerts, and J. Van Niekerk. 1989. Encroachment and
615 control of undesirable plants. *Veld management in the Eastern Cape* pages 73–89.

616 Turnbull, L., J. Wainwright, and R. E. Brazier. 2010. Changes in hydrology and erosion
617 over a transition from grassland to shrubland. *Hydrological Processes: An Interna-*
618 *tional Journal* **24**:393–414.

619 Van Auken, O. 2009. Causes and consequences of woody plant encroachment into western
620 North American grasslands. *Journal of environmental management* **90**:2931–2942.

621 Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual*
622 *review of ecology and systematics* **31**:197–215.

623 Veit, R. R., and M. A. Lewis. 1996. Dispersal, population growth, and the Allee ef-
624 fect: dynamics of the house finch invasion of eastern North America. *The American*
625 *Naturalist* **148**:255–274.

626 Wang, M.-H., M. Kot, and M. G. Neubert. 2002. Integrodifference equations, Allee
627 effects, and invasions. *Journal of mathematical biology* **44**:150–168.

628 Weiner, J. 1990. Asymmetric competition in plant populations. *Trends in ecology &*
629 *evolution* **5**:360–364.

- 630 Wells, P. V., and J. H. Hunziker. 1976. Origin of the creosote bush (*Larrea*) deserts of
631 southwestern North America. *Annals of the Missouri Botanical Garden* pages 843–861.
- 632 Whitford, W., E. Depree, and P. Johnson. 1980. Foraging ecology of two chihuahuan
633 desert ant species: *Novomessor cockerelli* and *Novomessor albigaster*. *Insectes Sociaux*
634 **27**:148–156.
- 635 Whitford, W. G. 1978. Structure and seasonal activity of Chihuahua desert ant commu-
636 nities. *Insectes Sociaux* **25**:79–88.
- 637 Wiernga, J. 1993. Representative roughness parameters for homogeneous terrain.
638 *Boundary-Layer Meteorology* **63**:323–363.
- 639 Yeaton, R. I., J. Travis, and E. Gilinsky. 1977. Competition and spacing in plant
640 communities: the Arizona upland association. *The Journal of Ecology* pages 587–595.