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3 **Choice of density dependent seedling**
4 **recruitment function affects predicted**
5 **transient dynamics: A case study with Platte**
6 **thistle**

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21 **Abstract** Modelers have to make choices about which functional forms to use for
22 representing model components, such as the relationship between the state of
23 individuals and their vital rates. Even though these choices significantly influence
24 model predictions this type of structural uncertainty has been largely ignored in
25 theoretical ecology. In this paper we use integral projection models (IPMs) for
26 Platte thistle as a case study to illustrate that the choice of functional form
27 characterizing density dependence in seedling recruitment has important
28 implications for predicting transient dynamics (short-term population dynamics
29 following disturbances). In one case the seedling recruitment function is modeled
30 as a power function, and in the other case we derive density dependence in
31 seedling recruitment from biological first principles. We chose parameter values
32 for the recruitment functions such that both IPMs predicted identical equilibrium

1 population densities and both recruitment functions fit the empirical recruitment
2 data sufficiently well. We find that the recovery from a transient attenuation, and
3 the magnitude of transient amplification, can vary tremendously depending on
4 which function is used to model density dependent seedling recruitment. When
5 we loosen the restriction of having identical equilibrium densities, model
6 predictions not only differ in the short-term but also in the long-term. We derive
7 some mathematical properties of the IPMs to explain why the short-term
8 differences occur.

9
10 **Keywords** *Transient dynamic; Density dependence; Integral projection model;*
11 *Seedling recruitment function; Mechanistic modeling; Michaelis-Menten function*

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1 **Introduction**

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3 For structured population models, where members of the population are classified by one or more
4 characteristic stages, most research has been focused on analyzing long-term, asymptotic
5 population characteristics, such as a population's asymptotic growth rate or equilibrium population
6 density. However, when a population is forced away from its equilibrium stage distribution by
7 disturbances such as environmental catastrophes or management actions, the subsequent dynamics
8 of this population can change considerably in the short-term (transient dynamics), making the
9 analysis of such dynamics extremely relevant (Hastings 2004). For example, sudden changes in
10 some vegetative distributions can significantly change the structure of associated animal
11 communities (Snyder 2009; Weller and Spratcher 1965). The impacts of such disturbances on
12 population dynamics can often not be elucidated with equilibrium analysis alone.

13 The majority of investigations of transients in discrete-time, structured population models
14 have focused on models that are density independent (Caswell, 2007; Caswell 2008; Koons et al.
15 2005; Tenhumberg et al. 2009; Townley et al. 2007; Townley and Hodgson 2008; Stott et al.
16 2010). However, many systems are driven by density dependent mechanisms, but the signal for
17 density dependence in empirical data sets is often weak. A typical example of this is the seedling
18 recruitment data of Rose et al (2005, Fig 1): the data are few, very noisy and collected over a
19 limited range of seed densities. It is challenging to find sensible functions that fit such noisy data
20 well, and commonly used criteria to choose among different candidate functions such as Akaike's
21 Information Criterion (AIC), or Bayesian information criterion can only provide a relative ranking
22 of "poor" fitting functions. Moreover, these statistical criteria do not consider the ability of a
23 function to project dynamics outside the range of observed data. This is particularly relevant if one
24 is interested in dynamics outside the range of data collection, which is often the case when
25 studying the effect of large perturbations that can cause transient dynamics. When projecting
26 dynamics outside the range of data collected we might consider functional forms that are derived
27 from first principles, but do not rank first based on information criteria, and evaluate the effect of
28 structural model uncertainty on model predictions.

29 In this paper we use the *density dependent* integral projection model (IPM) for Platte
30 thistle (*Cirsium canescens*) developed by Rose et al. (2005) as a case study to evaluate the impact
31 of structural model uncertainty on short-term behavior. Rose et al. (2005) represent density
32 dependent seedling recruitment with a power function of the form $f(x) = x^\nu$, where x is the
33 density of seeds produced by the population in one time-step, $f(x)$ is the density of seedlings that
34 result from these seeds and the parameter ν is fit to data. If $0 < \nu < 1$ (which is essential to
35 describe negative density dependent dynamics), the power function has mathematical properties
36 which include having an unbounded derivative for low seed densities and being unbounded for
37 large seed densities. These extreme values of x are outside the range of seed densities considered
38 in the statistical analysis of Rose et al. (2005). When studying transient dynamics, *extreme values*
39 *of x are highly relevant*. Therefore, we derived an alternative function for seedling recruitment
40 based on biological principles that takes into account these extreme values and ask the question:

1 How sensitive are the predicted transient dynamics to the choice of the function used to
2 characterize density dependent seedling recruitment? Our alternative function describes seedling
3 recruitment more realistically for extreme values of x , as recruitment is essentially linear for small
4 seed densities and essentially constant for large seed densities. The resulting function is identical
5 to the classical Michaelis-Menten, Beverton-Holt or Holling Type II functional response functions.
6 We will call it the Michaelis-Menten function for the remainder of the paper.

7 Other theoretical studies have emphasized that in many circumstances statistically well-
8 fitting nonlinear functions are not ecologically realistic (see, for instance, Cousens 1991;
9 Freckleton, et al 2008, Runge and Johnson 2002). However, this paper highlights the role that the
10 functional form of the density dependence plays in short-term, transient dynamics which, to our
11 knowledge, has not been addressed.

12 To create a consistent setting for our derivation, we will first give a detailed account of
13 the dimension of each function used in the IPM. We consider it desirable for a candidate
14 recruitment function to have dimensions that are consistent with the rest of the IPM. We will then
15 illustrate the differences in transient dynamics between the IPM using the power function and the
16 Michaelis-Menten function by simulating two ecological events. The first simulation will mimic
17 an ecological catastrophe, like a fire that destroys all above-ground plant biomass, where the initial
18 population will consist entirely of seedlings (recruited from surviving seeds left in the ground).
19 Second, we will simulate an ecological restoration project where the initial population consists of
20 large, adult plants. We show that both IPMs can yield surprisingly large differences in transient
21 dynamics even though the fit of the Michaelis-Menten function to the empirical data is comparable
22 to the power function (Fig. 1) and both IPMs predict the same equilibrium population density. We
23 derive mathematical properties of the two models that show why these differences occur and
24 further verify these results after loosening the restriction that the two models predict identical
25 equilibrium population densities.

27 **Model**

29 Density Dependent Integral Projection Model IPM for Platte thistle

31 An IPM can be used to describe how a population with a continuously-varying stage
32 structure changes in discrete time (Easterling et al. 2000). The use of IPMs in plant ecology has
33 grown tremendously over the last decade (Ramula et al. 2009). See Briggs et al. (2010) for a
34 tutorial on constructing IPMs. The population is characterized by a function, $n(x, t)$, where

$$35 \int_{x-\delta x}^{x+\delta x} n(y, t) dy \quad (1)$$

36 gives the total density of the population near stage x and time t , with dimension $plants(area)^{-1}$.
37 This function can be thought of as a continuous-stage analogue to population vectors $n(t)$ in
38 population projection matrix models (e.g. Caswell 2001). We have chosen to use an IPM because
39 the ability to capture the transient dynamics is often linked to model dimension (the number of life

1 history stages) (Tenhumberg et al. 2009; Stott et al. 2010). In a general IPM, the population
 2 $n(x, t)$ satisfies the integro-difference equation,

$$3 \quad n(x, t + 1) = \int_L^U K(x, y)n(y, t)dy, \quad (2)$$

4 where $K(x, y)$ is called the kernel of the IPM and L and U are the smallest and largest observed
 5 value for the stage, respectively. We decompose the kernel into two parts:

$$6 \quad K(x, y) = p_1(x, y) + p_2(x, y), \quad (3)$$

7 where $p_1(x, y)$ describes survival and growth, which models the probability of “movement” from
 8 stage y to stage x in one time-step. The “fecundity” portion of the kernel, $p_2(x, y)$, models the
 9 density of stage x individuals that are produced by stage y individuals.

10 We use a version of Rose et al.’s model (2005) that ignores the effect of seed predation
 11 (Briggs et al. 2010); this modification does not affect the way density dependence is implemented
 12 in the model. The natural logarithm of the plant’s root crown diameter is used as an indicator of
 13 plant size (the stage variable); the time-step is one year. We start by mentioning the dimension of
 14 each of the model components to contrast the two seedling recruitment functions (Michaelis-
 15 Menten and power function) on the basis of dimensional analysis. The Platte thistle population’s
 16 distribution, $n(x, t)$, has the dimension of $plants(size)^{-1}(area)^{-1}$. Let $s(y)$ and $f_p(y)$ be the
 17 survival and flowering probabilities, respectively, of members of the population with size y . If we
 18 call the growth function $g(x, y)$, where

$$19 \quad \int_{x-\delta x}^{x+\delta x} g(z, y)dz \quad (4)$$

20 is the probability of a size y plant growing to a size near x in one time-step (which is a probability
 21 distribution for each fixed y), then we have

$$22 \quad p_1(x, y) = s(y)(1 - f_p(y))g(x, y), \quad (5)$$

23 where the functions $s(y)$ and $f_p(y)$ are dimensionless, while $g(x, y)$ has the dimension of

$$24 \quad (size)^{-1} \text{ (with } \int_{x-\delta x}^{x+\delta x} g(z, y)dz \text{ being dimensionless).}$$

25 The probability of not flowering, $1 - f_p(y)$, is incorporated into the survival part of the
 26 kernel, because Platte thistle is a monocarpic plant and, as a consequence, flowering is fatal. The
 27 model assumes that survival, flowering and growth are independent events, and that seedling size
 28 is independent of the size of the mother plant (a low maternal effect on seedling size has also been
 29 reported for other plant species (Weiner et al. 1997; Sletvold 2002)).

30 The fecundity portion of the kernel is

$$31 \quad p_2(x, y) = p_e s(y) f_p(y) S_d(y) J(x), \quad (6)$$

1 where $S_d(y)$ is the number of seeds produced by members of the population with size y (with
 2 dimension of $(seeds)(plant)^{-1}$), and $J(x)$ is the probability distribution of the size of
 3 seedlings, with dimension of $(size)^{-1}$. The term p_e (with dimension of $plants(seed)^{-1}$) is the
 4 probability of a seed establishing to become a seedling by the next time-step, that is, the
 5 probability that a seed germinates and survives until the next population census. Seed
 6 establishment probability for Platte thistle is *density dependent* (Rose et al 2005). Thus, if $\gamma(t)$ is
 7 the density of seeds produced by the population at time t , the seed establishment probability is
 8 given by

$$9 \quad p_e(t) = \gamma(t)^{\nu-1}, \quad (7)$$

10 where the estimated value for ν in Rose et al. (2005) is 0.67, which is the value we use in this
 11 paper. The function describing the size structure of seedlings, $J(x)$, is independent of y , and from
 12 the construction of the kernel we see that the density of seeds produced is

$$13 \quad \gamma(t) = \int_L^U s(y) f_p(y) S_d(y) n(y, t) dy. \quad (8)$$

14
 15 Thus, the full density-dependent IPM is

$$16 \quad n(x, t+1) = \int_L^U p_1(x, y) n(y, t) dy + \int_L^U \gamma(t)^{\nu-1} J(x) s(y) f_p(y) S(y) n(y, t) dy. \quad (9)$$

17 More concisely,

$$18 \quad n(x, t+1) = \int_L^U p_1(x, y) n(y, t) dy + J(x) \gamma(t)^{\nu}. \quad (10)$$

19
 20 Notice that the model in Eq. 10 is the sum of a density independent growth and survival
 21 and density dependent seedling recruitment. We write a *general* seedling recruitment function as
 22 $f(\gamma(t)) = p_e(\gamma(t))\gamma(t)$, in order to stress that this function is the product of the seed
 23 establishment probability and the density of seeds at time t . When $p_e(\gamma(t))$ is as in Eq. 7, we
 24 have that $f(\gamma(t)) = \gamma(t)^{\nu} = p_e(\gamma(t))\gamma(t)$. We must note that some authors have used the term
 25 “recruitment” to mean the same as “establishment probability” (see, for instance, Runge and
 26 Johnson 2002). In this paper these terms are used to describe two distinct, albeit related, concepts,
 27 as seedling recruitment is the product of seed establishment and seed density.

28 In general, a seedling recruitment function $f(\gamma(t))$, has the dimension of
 29 $plants(area)^{-1}$, which is consistent dimensionally with the rest of the model. Hence $p_e(\gamma(t))$
 30 has the dimension of $plants(seed)^{-1}$. Since $\nu \in (0,1)$, the function $p_e(\gamma(t)) = \gamma(t)^{\nu-1}$ does
 31 not have these dimensions for *any choice of* $\nu \in (0,1)$. In the next section we derive a seedling

1 recruitment function from first principles so that every parameter has a clear biological
 2 interpretation from the dimensional analysis point-of-view.

3

4 Derivation of Seedling Recruitment Function

5

6 To mechanistically derive the seedling recruitment function, $f(\gamma(t))$, we follow in the spirit of the
 7 derivation of the Holling Type II functional response in classical predation theory (Holling 1959).
 8 We envision seeds participating in “predation of space”, with the analogy of “handling time” by
 9 Holling in classical predation theory becoming “handling space” in our derivation. In this model,
 10 we only consider *intraspecific* competition. In the Discussion section we will talk about how to
 11 include *interspecific* competition in this framework.

12 Let $N(t)$ be the density of seedlings that are recruited between time t and $t + 1$, i.e. the
 13 density of seeds produced that survive to become a seedling within one time-step. First, we make
 14 the assumption that the number of seedlings between time t and $t + 1$ increases with the space
 15 available for seeds to establish, $S(t)$, which has the dimension of *area*. Also assume that $N(t)$
 16 increases (as a function of $\gamma(t)$) with the establishing efficiency rate a , where a has the dimension
 17 $plants(seed)^{-1}(area)^{-1}$. A first attempt at a relationship between $N(t)$ and $\gamma(t)$ yields

$$18 \quad N(t) = aS(t)\gamma(t). \quad (11)$$

19 To obtain a more realistic relationship between $N(t)$ and $\gamma(t)$ it is reasonable to assume
 20 that the space available to establish will decrease with the number of seedlings, so $S(t)$ is
 21 decreasing with respect to $N(t)$. We envision a seed addition experiment where only seeds
 22 compete among themselves for the available microsite area. If we define the constant S_e to be the
 23 space taken up (as a proportion of the total space available) by one seed that establishes and
 24 becomes a seedling, where S_e has dimension $area(plant)^{-1}$, we can re-write $S(t)$ as follows:

$$25 \quad S(t) = S_{tot} - S_{tot}S_eN(t) = S_{tot}(1 - S_eN(t)), \quad (12)$$

26 where S_{tot} is a fixed characteristic of the population’s environment and is the total area of the space
 27 available for the plant population’s seeds to establish. Substituting Eq. 12 into Eq. 11 and solving
 28 for $N(t)$ yields:

$$29 \quad N(t) = \frac{aS_{tot}\gamma(t)}{1 + aS_{tot}S_e\gamma(t)}. \quad (13)$$

30 Or, more concisely,

$$31 \quad N(t) = \frac{\alpha\gamma(t)}{\beta + \gamma(t)}, \quad (14)$$

32 where

$$33 \quad \alpha = (S_e)^{-1}, \beta = (aS_{tot}S_e)^{-1}. \quad (15)$$

1 The dimensions of α and β are $plants(area)^{-1}$ and $seeds(area)^{-1}$, respectively. Eq. 14 is the
 2 Michaelis-Menten function. Notice that, if we let $N(t) = f(\gamma(t))$, we can write

$$3 \quad f(\gamma(t)) = \left(\frac{\alpha}{\beta + \gamma(t)} \right) \gamma(t) = p_e(\gamma(t))\gamma(t). \quad (16)$$

4 Using the Michaelis-Menten function for seedling recruitment, we can clearly interpret the
 5 parameters and their dimensions in a way that is consistent with the rest of the model. For
 6 example, the function $p_e(\gamma(t))$ has dimension of $plants(seeds)^{-1}$ and decreases to zero as the
 7 number of seeds grows to infinity, as one should expect in the dynamics of negative density
 8 dependent seed establishment. Also, when $\gamma(t) \approx 0$, we see that $p_e(\gamma(t)) \approx \alpha(\beta^{-1}) = \alpha S_{tot}$,
 9 which describes the probability of a seed establishing in the total absence of density-dependence.
 10 β is an analogue for the familiar half-saturation constant in classical predation theory
 11 (Vandermeer and Goldberg 2003), and is here the seed production needed to attain half of the
 12 maximum total seedling recruitment, α .

13 The Michaelis-Menten function is a limiting case of Duncan et al. (2009)'s derivation of a
 14 general seedling recruitment function, which considers "safe sites" for seeds to establish and
 15 makes assumptions about the distribution of seeds after flowering and dispersal. The derivation in
 16 this paper is considerably simpler and, given that we are not modeling space explicitly as a
 17 variable in the population, perhaps more appropriate for this setting.

18 For the remainder of this paper we call the IPM that uses the power function for seedling
 19 production the "power function" model, and we call the IPM that uses the Michaelis-Menten
 20 function the "mechanistic" model. Note that the survival, growth, seed production and distribution
 21 of seedlings portions remain identical in the two models, and therefore these names are simply to
 22 distinguish the way the seedling recruitment is implemented in the IPM's.

23 24 **Results**

25
26 To compare the two Platte thistle IPM's fairly, we initially calibrated the parameters of the
 27 Michaelis-Menten function to obtain the same equilibrium population density as the power
 28 function model (see Appendix A). Therefore, the subsequent comparisons in Example 1a and 1b
 29 are of two IPMs having identical equilibrium population densities and size distributions. The fit of
 30 the calibrated Michaelis-Menten to the empirical recruitment data was comparable to the fit of the
 31 power function used in Rose et al. (2005) (see Fig 1).

32 We define the transient function $T(t, \rho)$ to be the per-capita difference in the total
 33 population density from one time-step to another, dependent on the initial population distribution,
 34 $\rho(x)$. Mathematically,

$$35 \quad T(t, \rho) := \frac{\|n(\cdot, t)\| - \|n(\cdot, t-1)\|}{\|n(\cdot, t-1)\|}, \quad t = 1, 2, \dots, \quad (17)$$

36 where $\| \cdot \|$ refers the L^1 norm defined by

$$\|\varphi(\cdot, t)\| := \int_L^U \varphi(x, t) dx, \quad (18)$$

which equals the total population density of $\varphi(x, t)$, with dimension $plants(area)^{-1}$. This transient function definition is similar to the GR metric used in Koons et al. (2005) for matrix models and is a function of t and ρ alone, as $n(x, t)$ implicitly depends on the initial population ρ . The “ \cdot ” symbol indicates that the stage variable, x , is integrated away. This measurement of transients compares the population’s current total density with its total density *in the previous time-step*. We say that the population experiences a *transient attenuation* at time t_0 if $T(t_0, \rho) < 0$ and a *transient amplification* if $T(t_0, \rho) > 0$. Note that we can re-write the transient function as the per-capita growth rate minus unity. This makes clear our intention to have the cutoff between transient attenuation and amplification at zero. Therefore, using our definition, if a population has a transient attenuation (amplification), it has a smaller (larger) density than it had one time-step ago.

We have made certain to explicitly write that the transient function depends on the initial population distribution because the transient dynamics of a single-species, structured population tend to depend on the population structure that is remaining after the ecological disturbance corresponding to $t = 0$. For examples of this phenomenon in density independent matrix models see Townley et al. (2007) and Koons et al. (2005). Next, we illustrate that the stage structure of the initial population is the key determinant of the transient dynamics predicted by the Platte thistle IPMs and provide the proof in Appendix B. For a non-zero population $n(x, t)$, which solves the density-dependent IPM

$$n(x, t + 1) = \int_L^U p_1(x, y) n(y, t) dy + f(\gamma(t)) J(x), \quad n(x, 0) = \rho(x), \quad (19)$$

the value of the transient function at time $t_0 + 1$ can be re-written as

$$T(t_0 + 1, \rho) = E_{n(\cdot, t_0)}((1 - f_p(x))s(x)) - 1 + \frac{f(\|n(\cdot, t_0)\| E_{n(\cdot, t_0)}(c(x)))}{\|n(\cdot, t_0)\|}, \quad (20)$$

where $c(x) = s(x)f_p(x)S(x)$ and $E_{n(\cdot, j)}(z)$ is the expected value of z subject to the probability density function defined by $P(x, j) := n(x, j)(\|n(\cdot, j)\|)^{-1}$. More specifically, the initial value of the transient function is

$$T(1, \rho) = E_{\rho(\cdot)}((1 - f_p(x))s(x)) - 1 + \frac{f(\|\rho(\cdot)\| E_{\rho(\cdot)}(c(x)))}{\|\rho(\cdot)\|}. \quad (21)$$

This identity states that the transient function is the sum of expected probability of death (due to flowering and mortality) and expected per-capita seedling production. At equilibrium the transient function is roughly zero, and therefore per-capita seedling production offsets mortality. However, when a population is not at equilibrium we can expect that the right-hand side of Eq. 20 will not be zero.

1 Note that the presence of the expected values in Eq. 20 and Eq. 21 strengthens what is
 2 widely believed about the size distribution's impact on single-species transient dynamics. For
 3 example, in a plant population where the smallest plants have the lowest survival probability and
 4 produce the fewest seeds, one should expect that the largest transient attenuations would occur
 5 with an initial population largely consisting of small plants. This is due to the fact that the
 6 expected survival probability, seed production and subsequent seedling recruitment for small
 7 plants will be small. This will result in the first term of the transient function plus the per-capita
 8 seedling recruitment being small relative to unity, resulting in negative transient function values.

9 A surprising result in this paper is that the total population *density* alone can explain why
 10 the predicted transient dynamics differ between the two models. For instance, if the population
 11 density in the power function model becomes sufficiently low (as in transient attenuation) the
 12 mathematical properties of the power function force the transient function to have extremely high
 13 values. Notice that in the power function model the transient function can be re-written as

$$14 \quad T(t_0 + 1, \rho) = E_{n(\cdot, t_0)}((1 - f_p(x))s(x)) - 1 + \frac{E_{n(\cdot, t_0)}(c(x))^\nu}{\|n(\cdot, t_0)\|^{1-\nu}}. \quad (22)$$

15 Assume that the initial population distribution is a predetermined density, M , of
 16 seedlings, i.e. $\rho(x) = MJ(x)$. In subsequent time-steps, the only *new members* of the
 17 population are seedlings, distributed according to $J(x)$. Because not all seedlings survive to their
 18 second year (for example, $E_{J(\cdot)}((1 - f_p(x))s(x)) = 0.502$ in Rose et al. 2005) and grow grow to
 19 a much larger size the stage distribution stays roughly the same for small t (see Eq. 10). Let us
 20 assume that the total population *density* changes in the right hand side of Eq. 22 without changing
 21 the stage distribution at time t_0 . This implies that the expected values in Eq. 22 are also
 22 unaffected. When $\nu \in (0,1)$ Eq. 22, viewed as a function of $\|n(\cdot, t_0)\|$, is *unbounded* as $\|n(\cdot, t_0)\|$
 23 approaches zero. This is due to the fact that the derivative of the power function, $f'(x) = x^{\nu-1}$,
 24 goes to infinity as x approaches zero. Thus, for every positive real number N there exists a total
 25 population density $\|n(\cdot, t_0)\| = M_N$ such that for all total population densities *smaller* than M_N we
 26 have

$$27 \quad T(t_0 + 1, \rho) > N. \quad (23)$$

28 This conclusion in Eq. 23 states that, given a fixed stage distribution for the population, the power
 29 function model predicts that there exists a population density that ensures the beginning of a
 30 *recovery* (i.e the population density starts rapidly increasing towards the equilibrium), once the
 31 total population density dips *below* this value. For instance, in the power function model it is
 32 possible that a population of largely non-reproducing plants (seedlings) starts to grow once the
 33 population density drops below a particular threshold. We will illustrate this idea in Example 1a.

34 The previous mathematical artifact is not present in the mechanistic model, whose
 35 transient function can be written as

$$1 \quad T(t_0 + 1, \rho) = E_{n(\cdot, t_0)}(1 - f(x))E_{n(\cdot, t_0)}(s(x)) - 1 + \frac{\alpha E_{n(\cdot, t_0)}(c(x))}{\beta + \|n(\cdot, t_0)\| E_{n(\cdot, t_0)}(c(x))}. \quad (24)$$

2 When viewed as a function of $\|n(\cdot, t_0)\|$, Eq. 24 is a bounded function. Therefore, no threshold
 3 population density exists below which a population is guaranteed to increase. For instance, a
 4 population of seedlings cannot grow until some of the plants grow sufficiently large to reproduce.

5 When transient amplification occurs, the differences in the predictions of the two models
 6 stem from the properties of the two seedling recruitment functions when the seed production is
 7 greater than the equilibrium seed production $\gamma^* = \int_L^U s(y) f_p(y) S(y) n^*(y) dy$ (here $n^*(y)$ is the
 8 equilibrium population). Because the power function $f(x) = x^v$ goes to infinity as x goes to
 9 infinity, in theory the power function will eventually predict much larger seedling recruitment than
 10 the Michaelis-Menten function and thus, everything else being equal, the power function model
 11 will have larger densities than the mechanistic model when seed production is large. In Example
 12 1a and 1b we chose model parameters so that equilibrium populations of the power function model
 13 and the mechanistic model are the same (see Appendix A), thus

$$14 \quad (\gamma^*)^v = \frac{\alpha \gamma^*}{\beta + \gamma^*}. \quad (25)$$

15 Assume that γ^* in Eq. 25 is the largest seed production such that the two seedling recruitment
 16 functions intersect (as it is the Example 1a and 1b, see Fig A1). In a way that is analogous to the
 17 argument for transient attenuation, for any initial population $\rho(\cdot)$ and specified difference N
 18 between total population densities in the two models, there exists a seed production γ_N that elicits
 19 (at least) this difference at time $t = 1$. To see this, let $n_1(\cdot, t)$ and $n_2(\cdot, t)$ and solve Eq. 19 with the
 20 same initial condition $\rho(\cdot)$, but with different seedling recruitment functions $f_1(\cdot)$ and $f_2(\cdot)$.

21 Then, since the survival and growth portions of the kernel are the same for both models, one has

$$22 \quad \left(\|n_1(\cdot, 1)\| - \|n_2(\cdot, 1)\| \right) = |f_1(\gamma(0)) - f_2(\gamma(0))| \int_L^U J(y) dy. \quad (26)$$

23 We then have that

$$24 \quad \left\| \|n_1(\cdot, 1)\| - \|n_2(\cdot, 1)\| \right\| = |f_1(\gamma(0)) - f_2(\gamma(0))| \quad (27)$$

25 because $J(\cdot)$ is a probability distribution and the $f_i(\gamma(0))$'s are independent of x . If $f_1(\cdot)$ is the
 26 power function we have that if $\gamma(0) \rightarrow \infty$ it follows that $f_1(\gamma(0)) \rightarrow \infty$. In contrast, if $f_2(\cdot)$ is
 27 the Michaelis-Menten function, $\gamma(0) \rightarrow \infty$ implies that $f_2(\gamma(0)) \rightarrow \alpha$, which confirms the
 28 claim of the existence of a γ_N that elicits a difference of at least N between the two models.

29 Furthermore, because

$$30 \quad \gamma(0) = \|\rho(\cdot)\| E_{\rho(\cdot)}(c(x)), \quad (28)$$

1 it follows that, given an initial probability density function for the population, one can find

2 $\|\rho(\cdot)\|_N$ such that for $\|\rho(\cdot)\| > \|\rho(\cdot)\|_N$ we have

3
$$\|n_1(\cdot,1)\| - \|n_2(\cdot,1)\| > N. \quad (29)$$

4 In Example 1b we will assume a homogeneous initial population and display this result by
5 showing how increasing $\|\rho(\cdot)\|$ increases the difference between the predicted populations after
6 only one time-step. .

7

8 Example 1a: Transient attenuation

9

10 To illustrate the consequences of the preceding mathematical discussions for predicted transient
11 dynamics we first envision a brief ecological disturbance, like a fire, that wipes out the entire
12 population of plants, with the exception of seeds in the soil that germinate to become seedlings in
13 the following year, but does not significantly alter the long-term environmental conditions. While
14 this is clearly an oversimplification, the goal of this example is to merely evaluate if the way we
15 implement density dependence influences predicted transient dynamics.

16 To simulate this event, we will let $\rho(x) = MJ(x)$ be the initial population, which
17 consists entirely of seedlings, so $\rho(x)$ is the population distribution of $M \text{ seedlings}(\text{area})^{-1}$.
18 Very small plants do not reproduce and seed production increases with plant size (see Rose et al.
19 2005), but plants of all sizes can die. Thus, we expect that a population consisting entirely of
20 seedlings will decrease initially, before rising back to its equilibrium population density.
21 Accordingly, for small t both IPMs predict transient attenuation because $c(x)$ is increasing and
22 survival and the probability of not flowering are always below unity.

23 The main difference in transient dynamics between the two models is how quickly the
24 population increases to its equilibrium density following the disturbance event (= speed of
25 recovery from transient attenuation). We began our simulations with M values equal to
26 10, 15, 25 and 50 $\text{seedlings}(\text{area})^{-1}$ using identical initial size distributions of the seedlings,
27 $J(x)$ in each simulation. As expected, in both IPMs the population density values decline
28 initially (see $t = 1$ in Fig 2). However, the power function model predicts a faster recovery than
29 the mechanistic model and the smaller the M value the larger is the difference between the
30 predicted recovery patterns For example, if $M = 10$ and $t = 10$ the power function model
31 predicts a population that is 4.75 times larger than that of the mechanistic model. This is in
32 accordance with the mathematical observation in Eq. 23. Initially, the total population densities
33 and size distributions of the populations are very similar for both models. However, when the
34 population density becomes small enough, the transient function of the power function model has
35 large positive values (relative to the mechanistic model), and faster recovery begins (see $t = 1$
36 years in Fig 3).

37

38 Example 1b: Transient amplification

1
2 We expect transient amplification when the initial size distribution is skewed toward larger plants
3 with higher reproductive value relative to the stable size distribution because the seed production
4 $c(x)$ is increasing. We envision a restoration scenario where plants are grown in a greenhouse,
5 until they reach a large target size and then transplanted into the field. In this case the initial
6 population consists entirely of large plants. To simulate this hypothetical situation we used an
7 approximation to the Dirac Delta distribution (an explanation of the Dirac Delta distribution can be
8 found in Appendix C), centered at nine-tenths of U , the largest root-crown diameter in the
9 population. Thus, $\rho(x) = M\delta(x - 0.9U)$, with initial population densities, M , of 10, 15, 25,
10 and 50. As Fig 4 illustrates, the power function model predicts transient amplifications that are
11 much larger relative to the mechanistic model and this difference is more extreme for large initial
12 population densities. If recruitment is modeled by the power function the large seed densities
13 produced by a population of large plants correspond to larger seedling densities compared to
14 recruitment being modeled by the Michaelis-Menten function. This difference grows with the
15 initial density because, naturally, large initial populations of seed-producing plants correspond to
16 large seed production values, and thus when large seed production values are the input for an
17 *unbounded* power function the model subsequently predicts larger seedling densities that if we
18 used the (bounded) Michaelis-Menten function. For example, in our simulation a density of 50
19 large $plants(area)^{-1}$ produces 1021754 *seeds*. This is larger than the equilibrium seed
20 production of $\gamma^* = 111398$ *seeds* (see Appendix A for this calculation) and thus we would
21 expect from Eq. 29 that the differences in recruitment would be quite large. In fact, the power
22 function allows 1.03% of these seeds to become seedlings while the Michaelis-Menten function
23 allows only 0.32% of these seeds to become seedlings. This difference in seed establishment
24 probability corresponds to an order-of-magnitude difference in transient amplification between the
25 two models.

26
27 Example 2a: Transient attenuation in models without identical equilibrium populations.

28
29 Ecologists do not know the equilibrium population density, thus when deciding which function
30 best describes density dependent seedling recruitment given the data, ecologists will independently
31 estimate both parameters of the Michaelis-Menten function, rather than attempting to estimate the
32 parameters to obtain a desired equilibrium. This approach produces differences in predicting the
33 equilibrium dynamics and magnifies the difference in the short-term dynamics compared to the
34 models with forced equal equilibriums. So, for this example we used nonlinear regression analysis
35 in R (R Core Development Team 2006) to estimate both model parameters from the data in Rose
36 et al. (2005). Interestingly this revised Michaelis-Menten function (which we will call the revised
37 Michaelis-Menten function) predicts a much smaller saturation constant α (see Fig 5). This yields
38 a much smaller equilibrium seed production γ^* , and consequently a smaller equilibrium population

1 density ($\|n^*\| \sim 429 \text{ plants}(\text{area})^{-1}$). Since the revised equilibrium density is much closer
2 numerically to the density at $t = 0$ in simulations with similar initial conditions to Example 1a the
3 revised mechanistic model will converge to its equilibrium population density much faster.
4 However, the mathematical observation in Eq. 23 about the transient function still holds, as when
5 the initial population becomes smaller the difference between $T(1, \rho)$ in the two models grows
6 (Fig 6).

7

8 Example 2b: Transient amplification in models without identical equilibrium populations.

9

10 We used similar initial conditions as in Example 1b to compare the transient amplifications of the
11 two models. Allowing for different equilibrium population densities produces larger differences in
12 the short-term dynamics between the power function model and the revised mechanistic model
13 compared to the previous models that forced the same equilibrium dynamics. (Fig 7). As Eq. 29
14 suggests, the population density in the power function model can get very large in one time-step
15 (relative to the revised mechanistic model) due to the lack of a restrictive upper bound. In
16 contrast, the revised Michaelis-Menten function has a relatively low saturation constant, and the

17 equilibrium population recruitment is at saturation level, i.e. $\frac{\alpha\gamma^*}{\beta + \gamma^*} \approx \alpha$. This is because the

18 straight line $h(\gamma) = p_e^*(\gamma)$ intersects the revised Michaelis-Menten function well into its
19 asymptote (see Appendix A). This means that the total population density at $t + 1$ cannot grow
20 larger than the total population density at t plus the maximum seedling recruitment α , and
21 therefore population trajectories from the revised mechanistic model remain relatively constant.

22

23 Discussion

24

25 Using Platte thistle as a case study we have shown that the predicted transient dynamics can vary
26 considerably depending on how we implement density dependence in recruitment, even if the
27 equilibrium dynamics are the same. We have also shown that that these differences occur in
28 models where the parameters are fit independently. Through mathematical arguments we verify
29 that these differences in transient dynamics between these two models are due to the differences in
30 functional form, and not simply a product of parameter uncertainty, as the results in Eq. 23 and Eq.
31 29 are for general power functions and general Michaelis-Menten functions. So while some
32 parameter values may display these differences more drastically than others, the results in this
33 paper suggest that for some ecological outcomes the predicted transient dynamics will differ,
34 regardless of parameter values used, and these differences do not have a bound.

35

36 It is interesting to note that when the parameters in the Michaelis-Menten function were
37 fit independently, the resulting equilibrium population density ($\|n^*\| \sim 429 \text{ plants}(\text{area})^{-1}$)
38 was similar to the beginning population size reported in Fig 1 (a) in Rose et al. (2005) prior to the
invasion by *Rhinocyllus*. This would appear to build on the suggestion made in this paper that

1 mechanistic modeling, followed by standard methods of parameter estimation, offers the ideal
2 prospect for obtaining a useful model when the data are poor.

3 The importance of choosing the most appropriate functional form for density dependent
4 recruitment has been recognized in other contexts. For example, Runge and Johnson (2002) have
5 shown that the functional form used for recruitment can influence the optimal harvesting strategy
6 for duck populations in a nontrivial way. They argue that the differences between these functions
7 often lie outside the range of observed, or even anticipated, data and therefore statistical methods
8 are limited in determining what functional relationships in vital rates are most appropriate. To
9 address the effect of the resulting structural uncertainty on model predictions the authors advocate
10 for *active probing* of models that vary in their implementation of vital rates, which means
11 exploring model predictions outside the realm of data collection. The benefit of this active
12 scrutiny is often overlooked because “model validation” typically focuses on replicating *previously*
13 *observed phenomena* (Maki and Thompson 2006). In the study by Rose et al (2005) there were
14 no empirical recruitment data for very low or very high seed densities available and the two
15 alternative recruitment functions differ mainly in the unobserved data range (Fig 1). The
16 sensitivity of the predicted transient dynamics to the choice of the recruitment function highlights
17 the value of active probing of model components.

18 Density dependence occurs due to the regulatory nature of limited resources in a system.
19 The strength of density dependence should be highest at some carrying capacity, and population
20 growth should not be limited at low population density, resulting in essentially linear dynamics.
21 The Michaelis-Menten function is essentially linear for small seed densities (provided that β is
22 sufficiently large). This implies that the density dependence does not influence population
23 dynamics until the seed density is sufficiently high, which is what we expect to see. In contrast,
24 when using the power function seedling recruitment is never linear for low seed densities. Thus
25 the power function may poorly predict the dynamics at low density levels. In other words, while
26 the population might not be experiencing the biological effects of density dependence, we are still
27 predicting its dynamics subject to the *mathematical* effects of density dependence (Hastings 2004).
28 In Example 1a we discovered that the power function model’s transient function can become
29 arbitrarily large when the population’s density becomes sufficiently small (Eq. 23). This is due to
30 the fact that the power function’s derivative is unbounded for seed production densities close to
31 zero, which causes seed establishment *probability* to be greater than unity for small seed densities.
32 For example, if $\gamma(t) = 0.75$, then

$$33 \quad \gamma(t)^v = (0.75)^{0.67} = 0.82, \quad (30)$$

34 which implies that $p_e(t) = 1.09$, which is clearly false, as seed establishment probability needs
35 to be bounded above by a number smaller than unity to make sense. The *largest* seed
36 establishment value for the Michaelis-Menten function is much smaller than unity, as
37 $p_e(\cdot) \leq \alpha\beta^{-1} = 0.07$.

38 In the case where the total seed production is much larger than the available number of
39 microsites, a constant number of seedlings are recruited for each time-step. No such limiting value
40 will be obtained in the power function because it is unbounded for large seed values and the

1 number of seedlings always increases with the number of seeds produced. Even though models
 2 using the power function to represent density dependent recruitment predict equilibrium
 3 population densities, the lack of an upper bound for recruitment may still lead to poor predictions
 4 of annual seedling recruitment if populations are skewed toward individuals with high
 5 reproductive value. The result is an overestimation of the potential magnitude of transient
 6 amplification (Eq. 29, Fig 4, Fig 7). In contrast, the Michaelis-Menten function is more realistic in
 7 this situation because, as the number of seeds produced goes to infinity, the density of recruited
 8 seedlings approaches the constant α . This constant is determined by the number of available
 9 microsites.

10 Apart from being more realistic, deriving functional relationships from first principles
 11 allows us to incorporate other relevant ecological mechanisms such as interspecific competition for
 12 limited microsites. In the presence of interspecific competition, density dependence would
 13 intensify and the maximum recruitment density would be lower. We can expand our derivation of
 14 the Michaelis-Menten function and insert a term for interspecific competition. If we let the
 15 aggregate seed density of other species competing with Platte thistle be denoted by $\omega(t)$, then our
 16 Michaelis-Menten function would have the form (Mangel 2006):

$$17 \quad f(\gamma(t), \omega(t)) = \frac{\alpha\gamma(t)}{\beta + \gamma(t) + \omega(t)}. \quad (31)$$

18 This function has similar properties of the Michaelis-Menten function for seedling recruitment,
 19 that is $f(\gamma(t), \omega(t))$ is close to linear for low $\gamma(t) + \omega(t)$ values and is roughly constant if $\gamma(t)$ is
 20 becomes large. One additional property of $f(\gamma(t), \omega(t))$ is that it becomes small if $\omega(t)$
 21 becomes large, because all microsites are occupied by the competing species. In contrast, the
 22 power function has no similar, intuitive extension for incorporating interspecific competition.

23 We have shown that the choice of the functional forms such as density dependent
 24 recruitment can have profound effects on predicted transient dynamics. This suggests that more
 25 emphasis should be placed on functional relationships that are derived based on mechanistic
 26 ecological principles.

27

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29

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35

36 **Appendix A: Calculating parameters to ensure common equilibrium values**

37

38 This section demonstrates how to find the parameter values for the seedling recruitment function in
 39 the mechanistic model that ensures that the power function and mechanistic model have a common

1 equilibrium population. For our particular model, Rebarber et al. (to appear) ensure that this
 2 equilibrium population exists for Eq. 19 and is globally stable, independent of non-zero initial
 3 population. To find this equilibrium population we begin by writing Eq. 19 in abstract form. To
 4 do this, we define the bounded operator $A_0 : L^1(L, U) \rightarrow L^1(L, U)$, the bounded functional
 5 $c^T : L^1(L, U) \rightarrow \mathfrak{R}$ and the $L^1(L, U)$ vector b by

$$6 \quad A_0 u = \int_L^U p_1(\cdot, x) u(x) dx, \quad c^T u = \int_L^U c(x) u(x) dx, \quad b = J(x). \quad (A1)$$

7 In this abstraction A_0 is the survival/growth operator, c^T is the reproductive functional and b is the
 8 distribution of newborns. We can now write our model as

$$9 \quad n(x, t + 1) = A_0 n(x, t) + b f(c^T n(x, t)) = A_0 n(x, t) + p_e (c^T n(x, t)) b c^T n(x, t). \quad (A2)$$

10 To calculate the equilibrium population we first need the concept of the stability radius of
 11 the real, positive system (A_0, b, c^T) . This is the smallest positive number p_e^* such that the
 12 spectral radius of the operator $A_0 + p_e^* b c^T$ is equal to unity. It is proved in Hinrichsen and
 13 Pritchard (2005) that p_e^* is given by the formula

$$14 \quad p_e^* = (c^T (I - A_0)^{-1} b)^{-1}. \quad (A3)$$

15 Suppose that f is increasing, concave down and $f(0) = 0$, and let γ^* be the solution of the
 16 equation

$$17 \quad p_e^* = p_e(\gamma). \quad (A4)$$

18 It is shown in Rebarber et al. (to appear) that the equilibrium population is given by the formula

$$19 \quad n^*(x) = (p_e^* \gamma^*) (I - A_0)^{-1} b, \quad (A5)$$

20 and that γ^* is the limiting seed production. Using the kernel functions in Table 2 of Rose et al.
 21 (2005), we compute that $p_e^* = 0.0216$, which we note is independent of the choice of seedling
 22 recruitment function $f(\gamma(t)) = p_e(\gamma(t))\gamma(t)$. To find the limiting seed production, γ^* , for both
 23 models, we solve Eq. A4. *This equality is what we need to match in the two seedling recruitment*
 24 *functions to obtain identical equilibrium populations.* For the power function model Eq. A4
 25 becomes

$$26 \quad (\gamma^*)^{-0.33} = 0.0216, \quad (A6)$$

27 from which we obtain $\gamma^* = 111397.68$. To match the mechanistic model we need to choose
 28 parameter values α and β in the Michaelis-Menten function in Eq. 14 such that $p_e^* = p_e(\gamma^*)$,
 29 where $\gamma^* = 111397.68$ and $p_e^* = 0.0216$. The Michaelis-Menten function has two parameters,
 30 which will allow us to use one parameter to ensure that $\alpha(\beta + \gamma^*)^{-1} = p_e^*$, with one additional
 31 parameter left to fit the empirical recruitment data in Fig 4 of Rose et al (2005). In this paper we

1 will allow β to be the free parameter, to be fitted to data, and solve for α in terms of β to obtain
 2 the common equilibrium population. In particular $\alpha = 0.0216(111397.68 + \beta)$. Finally, we
 3 used nonlinear regression to obtain $\beta = 49741$ from the data from Fig 4 of Rose et al. (Fig 1).

4 The calculation of p_e^* and all other simulations of the IPMs in this paper use the
 5 numerical integration techniques described in Ellner and Rees (2006). All numerical techniques in
 6 this paper were carried out using the statistical software R (R Development Core Team 2006) and
 7 codes are available upon request.

8

9 **Appendix B: Proof of the identity in equation Eq. 18**

10

11 To prove the identity in Eq. 20 we must first explicitly write the definition for the transient
 12 function at time $t_0 + 1$ with a given initial population $\rho(x)$. By the definition of $p_1(x, y)$ in Eq. 5
 13 and $P(y, t_0) := n(y, t_0) \left(\|n(\cdot, t_0)\| \right)^{-1}$ we have

14

$$15 \quad T(t_0 + 1, \rho) = \frac{\left\| \int_L^U p_1(\cdot, y) n(y, t_0) dy + f(\gamma(t)) J(\cdot) \right\| - \|n(\cdot, t_0)\|}{\|n(\cdot, t_0)\|} \quad (B1)$$

$$16 \quad = \iint_{L,L}^U s(y) (1 - f_p(y)) g(x, y) P(y, t_0) dy dx + \frac{f(\gamma(t))}{\|n(\cdot, t_0)\|} \int_L^U J(x) dx - 1 \quad (B2)$$

$$17 \quad = \iint_{L,L}^U s(y) (1 - f_p(y)) g(x, y) P(y, t_0) dy dx + \frac{f(\gamma(t))}{\|n(\cdot, t_0)\|} - 1, \quad (B3)$$

18 as the integral of the probability density function $J(x)$ is equal to unity. Since we are assuming
 19 that the functions in the kernel are all positive, sufficiently smooth functions, with $f_p(y) < 1$ for
 20 every y , we can use the Fubini-Tonelli Theorem (Folland 1999) to change the order of the
 21 remaining integral. Therefore:

$$22 \quad \iint_{L,L}^U s(y) (1 - f_p(y)) g(x, y) P(y, t_0) dy dx = \iint_{L,L}^U s(y) (1 - f_p(y)) g(x, y) P(y, t_0) dx dy \quad (B4)$$

$$23 \quad = \int_L^U s(y) (1 - f_p(y)) P(y, t_0) \int_L^U g(x, y) dx dy = \int_L^U s(y) (1 - f_p(y)) P(y, t_0) dy, \quad (B5)$$

24 as $g(x, y)$ is a probability distribution for each fixed y . By the definition of $P(y, t_0)$ we see that
 25 the right-hand side of Eq. B5 equals $E_{n(\cdot, t_0)}(s(y)(1 - f_p(y)))$. Finally note that, for every t ,

26

$\gamma(t)$ has the property that

$$27 \quad \gamma(t) = \int_L^U c(y) n(y, t) dy = \|n(\cdot, t)\| E_{n(\cdot, t)}(c(y)), \quad (B6)$$

1 which completes the proof.

2

3 **Appendix C: Notes on the Dirac Delta distribution**

4

5 When used to model a structured population, the Dirac Delta distribution is the continuous-stage
6 analogue of a population vector that has zeros in all but one entry. In other words, the Dirac Delta
7 distribution centered at a , written $\delta(x - a)$, roughly describes a population that is entirely of
8 members whose stage variable equals a . Formally, $\delta(x - a)$ is the limit of a sequence of strongly
9 peaked functions of the form:

$$10 \quad \delta_n(x) = \begin{cases} 0 & \text{for } x < a - \frac{1}{2n} \\ n & \text{for } a - \frac{1}{2n} < x < a + \frac{1}{2n} \\ 0 & \text{for } x > a + \frac{1}{2n} \end{cases} \quad (C1)$$

11 as $n \rightarrow \infty$. $\delta(x - a)$ has the property that

$$12 \quad \int_{-\infty}^{\infty} \phi(x) \delta(x - a) dx = \phi(a) \quad (C2)$$

13 for all sufficiently smooth functions $\phi(x)$ (Logan 2006). More specifically, if one allows
14 $\phi(x) = 1$, then we see that $\delta(x - a)$ is a probability density function and

$$15 \quad E_{\delta(x-a)}(\phi(x)) = \phi(a). \quad (C3)$$

16

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 14

15 **Fig 1** The relationship between seedling recruitment in year $t + 1$ and estimated seed production in
 16 year t . We digitized the data from Fig 4 in Rose et al. (2005) and calculated the parameter ν in the
 17 power function to obtain an estimate of the AICc (AIC with a correction for finite sample sizes)
 18 value. Our estimate for the parameter ν ($\nu = 0.654$) deviates only by 2% from the one reported by
 19 Rose et al (2005, $\nu = 0.67$); The AIC values of the power function from the digitized data (AICc =
 20 138.4) and the Michaelis-Menten function (AICc = 139.3) are similar. The dotted curve is the
 21 power function ($f_1(x) = x^{0.67}$), and the solid curve the Michaelis-Menten function
 22 ($f_2(x) = 3482x / (49741 + x)$). In Appendix A we describe parameter estimation procedure
 23 of the Michaelis-Menten function.
 24

25 **Fig 2** Predicted transient population dynamics for the two Platte thistle models resulting from
 26 simulating the ecological event in Example 1a. The initial densities, M , are (a) 10 (b) 15 (c) 25
 27 and (d) 50 seedlings/area; in each simulation the size distribution of the seedlings was identical to
 28 that reported in Rose et al. (2005).
 29

30 **Fig 3** Predicted transient function values for the two Platte thistle models resulting from simulating
 31 the ecological event in Example 1b. The initial densities, M , are (a) 10 (b) 15 (c) 25 and (d) 50
 32 seedlings/area; in each simulation the size distribution of the seedlings was identical to that
 33 reported in Rose et al. (2005).
 34

35 **Fig 4** Predicted total population densities for the two Platte thistle models resulting from
 36 simulating the ecological event in Example 1b. The initial densities, M , are (a) 10 (b) 15 (c) 25
 37 and (d) 50; in each simulation M was distributed according to the Dirac Delta distribution centered
 38 at nine-tenths of the largest observable plant's size. The dashed line illustrates the equilibrium
 39 population density (~ 5082 plants/area). For more on the Dirac Delta distribution, see Appendix
 40 C.

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Fig 5 The relationship between seedling recruitment in year $t + 1$ and estimated seed production in year t . The dotted curve remains the power function $f_1(x) = x^{0.67}$ as in Rose et al. (2005) and the

solid curve the revised Michaelis-Menten function fitted independently $f_2(x) = \frac{219.6x}{756.7 + x}$.

Note that the revised Michaelis-Menten function appears to be approaching its asymptote closer to the range of observable seed production. The AICc value for the revised Michaelis-Menten function (AICc = 140.6) is very similar to that of the power function of the digitized data in Rose et al. (2005) (AICc = 138.4) and the original Michaelis-Menten (AICc = 139.3) function used in Example 1a and 1b.

Fig 6 Predicted transient function values for the power function model and the revised mechanistic model resulting from simulating the ecological event in Example 2a. The initial densities, M , are (a) 0.25 (b) 0.5 (c) 0.75 and (d) 1 seedlings/area; in each simulation the size distribution of the seedlings was identical to that reported in Rose et al. (2005).

Fig 7 Predicted total population densities for the power function model and the revised mechanistic model resulting from simulating the ecological event in Example 2b. The initial densities, M , are (a) 5 (b) 10 (c) 15 and (d) 20; in each simulation M was distributed according to the Dirac Delta distribution centered at nine-tenths of the largest observable plant's size.

Fig A1 The relationship between seedling recruitment in year $t + 1$ and estimated seed production in year t . The intersection of the two recruitment functions with $h(x) = p_e^*x$ elicits the equilibrium seed production γ^* . We used this intersection to find the equilibrium population density (see Appendix A). Note that the equilibrium seed production is much larger than the observed data in Rose et al. (2005), which are indicated by the dots near the origin.