

The Effect of Habitat Fragmentation on Plant Communities in a Spatially-Implicit Grassland Model

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Cover Page Footnote

We would like to thank Forest Isbell, of Cedar Creek Ecosystem Science Reserve in Minnesota, for his time and tour of the research sites, and Lauren Sullivan for her valuable feedback throughout the project and for sharing data. A special thanks to our advisor, Kate Meyer, for her mentorship throughout the project.

The Effect of Habitat Fragmentation on Plant Communities in a Spatially-Implicit Grassland Model

By *Mika Cooney, Benjamin Hafner, Shelby Johnson, and Sean Lee*

Abstract. The spatially implicit Tilman-Levins ODE model helps to explain why so many plant species can coexist in grassland communities. This now-classic modeling framework assumes a trade-off between colonization and competition traits and predicts that habitat destruction can lead to long transient declines called “extinction debts.” Despite its strengths, the Tilman-Levins model does not explicitly account for landscape scale or the spatial configuration of viable habitat, two factors that may be decisive for population viability. We propose modifications to the model that explicitly capture habitat geometry and the spatial pattern of seed dispersal. The modified model retains implicit space and is in fact mathematically equivalent to the Tilman-Levins model in the single species case. But its novel interpretation of a habitat destruction parameter better quantifies seed loss due to edge effects in fragmented habitats and results in different predictions than the Tilman-Levins model. In particular, the seed-loss model predicts that species with strong dispersal traits may be most vulnerable to extinction in small habitat fragments.

1 Introduction

Urban development and agriculture have fragmented and reduced grassland ecosystems, prompting mathematical models that describe plant populations after habitat destruction. The Tilman-Levins model, hereafter referred to as the Tilman model, is a spatially implicit collection of ordinary differential equations, developed by Levins as a metapopulation model [4] and modified by Tilman to predict extinctions due to habitat loss [10]. The Tilman model is based on a hierarchical framework that ranks species in order from best local competitor (species 1) to worst local competitor (species n) based on their ability to compete for a limiting resource, such as sunlight, soil nitrogen, or water. The model shown below can be used for anywhere from one species’ response to habitat destruction, to the generalized interactions among n species subject to habitat destruction [5, 8].

Mathematics Subject Classification. 92D40

Keywords. Habitat fragmentation, extinction debt, spatially implicit, grasslands, ODE

$$\begin{aligned}
\frac{dp_1}{dt} &= c_1 p_1 (1 - D - p_1) - m_1 p_1 \\
\frac{dp_2}{dt} &= c_2 p_2 (1 - D - p_1 - p_2) - m_2 p_2 - c_1 p_1 p_2 \\
&\vdots \\
\frac{dp_i}{dt} &= c_i p_i \left(1 - D - \sum_{j=1}^i p_j\right) - m_i p_i - \sum_{j=1}^{i-1} c_j p_j p_i \\
&\vdots \\
\frac{dp_n}{dt} &= c_n p_n \left(1 - D - \sum_{j=1}^n p_j\right) - m_n p_n - \sum_{j=1}^{n-1} c_j p_j p_n
\end{aligned} \tag{1}$$

In equations (1), p_i is the proportion of sites in a spatial habitat occupied by plant species i . The parameters c_i and m_i control colonization and mortality rates respectively, and the parameter D is the proportion of sites that have been destroyed and are therefore no longer viable for any plant species to occupy.

The assumption built into the competitive hierarchy is that species i will always displace species j when $i < j$. For example, species 2 can colonize any site in the habitat that is unoccupied or occupied by species 3, 4, 5, ... n because it can outcompete these poorer competitors for the limiting resource. But species 2 cannot colonize sites that it already occupies, sites occupied by species 1, or sites that have been destroyed. Therefore, the total proportion of sites that species 2 can colonize is $1 - D - p_1 - p_2$. The lower a species is in the competitive hierarchy, the larger the number of superior competitors that reduce its available sites to colonize and displace it from sites it already occupies. Poorer competitors are only able to survive in this model through superior colonization abilities (higher c values), which allow them to reach empty sites first and fill the gaps left by the better competitors. Better colonizers often release more seeds that travel farther compared to better local resource competitors [7]. This type of modeling framework is known as a competition-colonization trade-off model [4]. It allows for biodiversity in a habitat when a better competitor is a worse colonizer, and a worse competitor survives by being a better colonizer.

One of the Tilman model's important contributions to ecology is its ability to predict how much habitat destruction, D , a species can withstand before it begins to suffer deterministic extinction. The model also highlights the possibility that populations decline slowly prior to extinction, a phenomenon known as an "extinction debt" [10]. The Tilman model predicts that the best local competitor is most vulnerable to extinction, and will face extinction debt exactly when D is equal to the percentage of habitat it occupies at equilibrium before any destruction occurs [9]. However, while the parameter D is an important addition to the model, it does not account for the scale and geometry

of the destroyed habitat, thus ignoring the impact of habitat fragmentation [1, 2]. For example, Figure 1 displays two different habitat configurations where $D = 0.5$ for both plots.

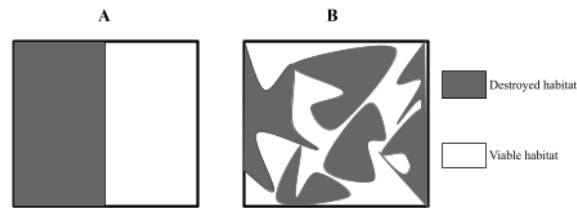


Figure 1: Two habitat configurations with $D = 0.5$

Both of these habitats have the same amount of viable space, yet previous studies [1] suggest that these habitats may lead to different population outcomes. Due to the smaller fragments of available space, habitat B has more edge length, which can lead to increased seed loss. When too many plants of a given species are near the edge of the viable region, a significant portion their seeds may end up landing in the destroyed region. This phenomenon effectively reduces the colonization ability of that species, pushing it closer to extinction. Yet in the Tilman modeling framework, both of these habitat configurations are mathematically equivalent, with the habitat destruction parameter set at $D = 0.5$ for both. A resulting Tilman model of the form (1) would predict the same dynamics for both plots.

In an attempt to better account for edge effects and habitat fragmentation, we adapt the Tilman model to take into account the portion of seeds each species loses as a result of landing outside the viable habitat. We use f to denote the fraction of a given species' seeds that are expected to land within the viable habitat. This seed retention factor can be predicted based on the spatial pattern of seed dispersal for individual species in combination with the geometry of viable habitat. By multiplying each species' colonization ability c_i by its seed retention factor f_i , we develop a model that remains spatially implicit and similar to the Tilman model, but accounts for habitat fragmentation instead of simply destruction. In this paper, we describe the modified Tilman model, which we call the "seed-loss model," discuss the computation and ecological significance of the new parameters, and include an example with plant data from the Cedar Creek Ecosystem Science Reserve in Minnesota to predict the effects of habitat destruction and fragmentation on Midwestern grassland species.

2 Seed-Loss Model

The seed-loss model is an n -species system of spatially implicit ordinary differential equations that tracks the proportion of viable habitat occupied by each species with

respect to time. We will discuss the one species case first and then generalize to an arbitrary number of species.

2.1 Single Species

The seed-loss model is built on the foundation of the original Levins metapopulation model [4]

$$\frac{dp}{dt} = cp(1 - p) - mp, \quad (2)$$

which Tilman later modified with the addition of the habitat destruction parameter D . We start by interpreting (2) in the case of a single habitat occupied by a single plant species. In this case, p represents the fraction of total viable sites in the habitat which are currently occupied. The rate of change of p consists of both propagation into unoccupied sites (colonization) and plant deaths (mortality). The colonization parameter c describes each plant's ability to produce and disperse viable seeds. Thus, cp represents the maximum colonization ability of all plants and $1 - p$ represents the fraction of seeds that land in unoccupied sites. The mortality parameter m describes the per capita plant death rate. Together, the colonization and mortality terms define a simple first-order, non-linear, ordinary differential equation with a stable equilibrium $p = 1 - m/c$. Because $p < 1$ at equilibrium, there is room for other species to live in the remaining portion m/c of the habitat. This makes the Levins model well suited to describing the coexistence of multiple species in one habitat, a strength retained by the Tilman model and also by the seed-loss model.

The seed-loss model's key point of departure from the Tilman model is its method for quantifying habitat destruction. Whereas the Tilman model focuses on the percentage of land destroyed D , the seed-loss model focuses on the percentage of seeds lost. The highly fragmented landscapes that often result from habitat destruction can lead to a significant portion of seeds landing on sites that are no longer viable. To quantify this phenomenon, let f denote the fraction of seeds that land within the viable habitat. Then $1 - f$ is the fraction of seeds that land in a destroyed region of the habitat that is no longer viable or outside the original habitat altogether. We account for seed loss by multiplying the species' colonization ability c by its "seed retention factor" f :

$$\frac{dp}{dt} = cfp(1 - p) - mp. \quad (3)$$

Note that c depends only on the viable seed production ability of the species in question, whereas f depends on the interplay between the spatial dispersal pattern of those seeds and the geometry of the site. For example, a species with seeds that often carry long distances on the wind would be more prone to seed loss, meaning it might have a low f value if constrained to too a small habitat. Generally speaking, a species will have a

lower f value in a small or fragmented habitat and a higher f value in a large continuous habitat. Hypothetically, an infinite habitat with no edges would achieve $f = 1$.

The single-species seed-loss model, as formulated in equation (3), is equivalent to the Tilman model with the substitution $f = 1 - D$ and $p = \hat{p}/(1 - D)$, where p corresponds to the seed-loss model and \hat{p} corresponds to the Tilman model (see Appendix I). But with multiple species, the correspondence between the seed-loss model and the Tilman model becomes more tenuous.

2.2 Multiple Species

The seed-loss model (3) generalizes to the n -species case in much the same way that the Tilman model does:

$$\begin{aligned}
 \frac{dp_1}{dt} &= c_1 f_1 p_1 (1 - p_1) - m_1 p_1 \\
 \frac{dp_2}{dt} &= c_2 f_2 p_2 (1 - p_1 - p_2) - m_2 p_2 - c_1 f_1 p_1 p_2 \\
 &\vdots \\
 \frac{dp_i}{dt} &= c_i f_i p_i \left(1 - \sum_{j=1}^i p_j\right) - m_i p_i - \sum_{j=1}^{i-1} c_j f_j p_j p_i \\
 &\vdots \\
 \frac{dp_n}{dt} &= c_n f_n p_n \left(1 - \sum_{j=1}^n p_j\right) - m_n p_n - \sum_{j=1}^{n-1} c_j f_j p_j p_n
 \end{aligned} \tag{4}$$

Species are ranked $1, 2, \dots, n$ according to their ability to compete locally for a limiting resource, such as soil nitrogen or water. Like in the Tilman model, if species j produces a seed that lands and sprouts in a site currently occupied by species i , species j will successfully displace species i as long as $j < i$. This displacement is represented in (4) as the interaction terms $\sum_{j=1}^{i-1} c_j f_j p_j p_i$. Conversely, if one of species i 's seeds lands and sprouts in a site already occupied by species $j \leq i$, that seedling would not be able to grow, since the existing plant of species j would not leave enough of the limiting resource. This is reflected in (4) by the sum $\sum_{j=1}^i p_j$ inside the parenthesis, reducing species i 's available space for colonization.

Although the single-species seed-loss model is equivalent to the single-species Tilman model with a simple substitution, this is only true in the multi-species case if the seed retention factors f_i are the same for every species (see Appendix I). In practice, it is unlikely that every species would have the same seed retention factor, because f is highly dependent on spatial seed dispersal patterns, which can differ significantly from species to species. These differences are most pronounced in small or highly fragmented habitats. For example, a species in a small habitat whose seeds typically travel long

distances may retain only a tiny fraction of its seeds, whereas a species with very short range seed dispersal could retain almost all of its seeds in the same habitat. In large and continuous habitats, these differences in spatial seed dispersal patterns are less important because every species' seed retention factor is closer 1. This indicates that the seed-loss model stands out most from the Tilman and Levins models in small or highly fragmented habitats.

2.3 Computing Seed Retention Factors

In this section, we explain how to numerically estimate a species' seed retention factor f in a specific habitat. In order to accurately predict f , we need to know two things: the spatial dispersal pattern of seeds, and the geometry of the viable habitat. The habitat geometry, which we will operationalize as a region $H \subset \mathbb{R}^2$, is relatively easy to determine from a map or aerial photograph. But the spatial dynamics of seed dispersal are harder determine. When a plant drops a seed, how far and in what direction will the wind carry it? Where will it land?

The probability distribution describing where one plant's seeds are most likely to land is called that plant's dispersal kernel. The dispersal kernel can be determined experimentally by observing where most of a plant's seeds end up, or it can be predicted theoretically based on typical wind conditions, the aerodynamic properties of the seeds, seed mass, and the height from which the seeds are released [7]. Mathematically, we will treat the dispersal kernel as a two-dimensional probability density function $g(x, y)$ where the vector (x, y) is a seed's horizontal displacement from the original location of the plant that dropped it.

Assuming $g(x, y)$ and H are both known, f can be computed in two steps:

1. Focus on a single plant located at (x_p, y_p) . Use the dispersal kernel to calculate that specific plant's seed retention factor, denoted f_{x_p, y_p} .
2. Average f_{x_p, y_p} over all possible plant locations $(x_p, y_p) \in H$ to estimate the species' overall seed retention factor, f .

To accomplish the first step, integrate g over all viable sites $(x_s, y_s) \in H$ where a seed can land to get the probability that a given seed will stay within H .

$$\text{[Step 1]} \quad f_{x_p, y_p} = \iint_{(x_s, y_s) \in H} g(x_s - x_p, y_s - y_p) dx_s dy_s$$

Note that the dispersal kernel g has been centered on the location of the single plant at (x_p, y_p) , so f_{x_p, y_p} represents the fraction of that particular plant's seeds expected to stay within H . Towards step 2, we assume that every plant produces the same number of seeds and that plants are evenly distributed in H . Then the species' total seed retention factor f is the average of each individual plant's seed retention factor f_{x_p, y_p} . This average

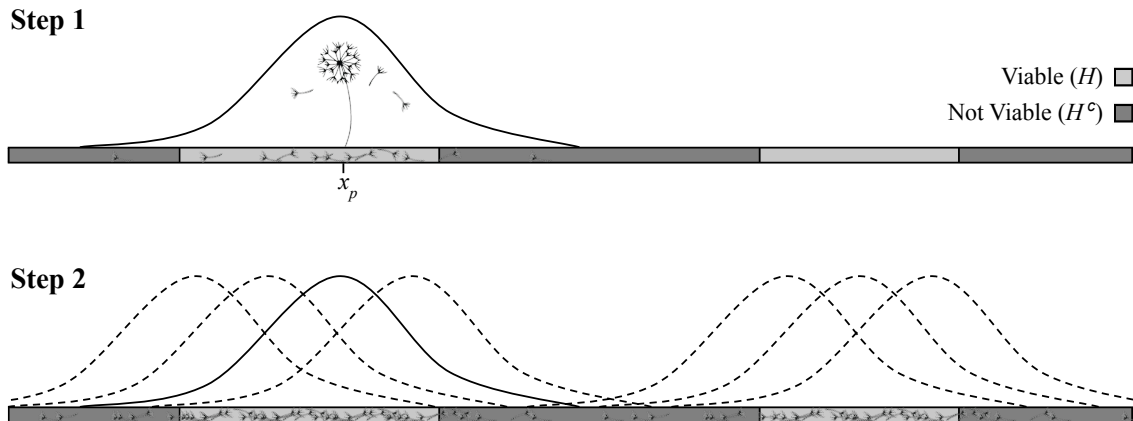


Figure 2: A visual demonstration of computing f in the one dimensional case. The curve in Step 1 represents the dispersal kernel for a single plant at x_p . This dispersal kernel can be integrated over the viable habitat H to find that particular plant's seed retention factor f_{x_p} . In Step 2, the seed retention factors are averaged over all possible plant locations $x_p \in H$, resulting in the total fraction f of all seeds that land within the viable habitat.

can be computed by integrating f_{x_p, y_p} over all $(x_p, y_p) \in H$ and then dividing by the total area A of H .

$$[\text{Step 2}] \quad f = \frac{1}{A} \iint_{(x_p, y_p) \in H} \iint_{(x_s, y_s) \in H} g(x_s - x_p, y_s - y_p) dx_s dy_s dx_p dy_p \quad (5)$$

While this integral is intractable analytically for all but the most basic g and H , it is relatively easy to approximate using numerical methods. For the example in the following section, we employ Wolfram Mathematica 12's `NIntegrate` function. The code we used to approximate the integral, along with code for modeling the ordinary differential equations (4), is included with the online version of this paper.

Once the habitat geometry and a given species' dispersal kernel are known, (5) gives that species' seed retention factor. The seed retention factors for all the species, in combination with colonization and mortality rates, fully parameterize the ordinary differential equations (4), which can then be used to model the population dynamics of the system. Figure 3 illustrates this process.

3 Illustrative Example

As a demonstration of the seed-loss model, we investigate a hypothetical two-species scenario. Suppose big bluestem (*Andropogon gerardii*) and common milkweed (*Asclepias syriaca*) both occupy a small grassland habitat in which soil nitrogen is the limiting resource. Big bluestem is a very good nitrogen competitor, so it will be species 1 in the

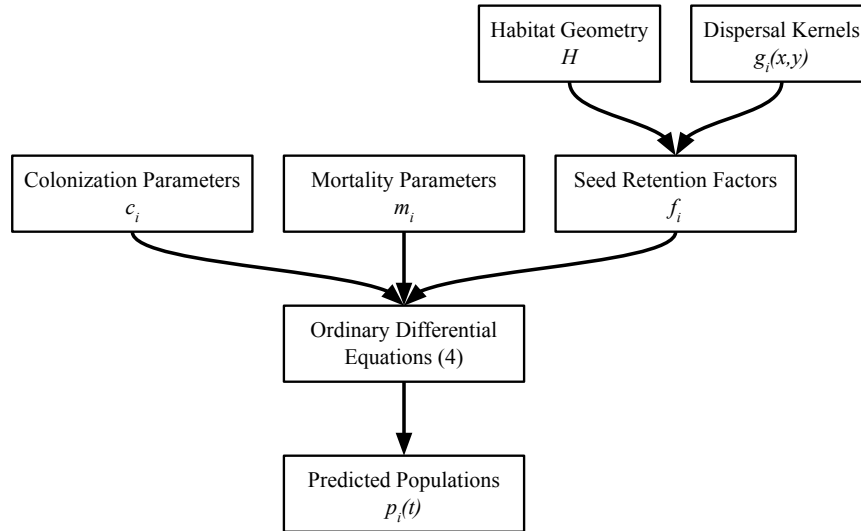


Figure 3: The seed-loss model requires parameters c_i , m_i , and f_i for each species i . We describe a method for computing the seed retention factors f_i from the habitat geometry H and the species' dispersal kernels $g_i(x, y)$. Methods for computing the colonization and mortality parameters c_i and m_i are beyond the scope of this paper.

seed-loss model's competitive hierarchy. As species 2 in the model, milkweed must rely on its superior colonization traits to survive. Specifically, milkweed produces significantly more seeds than big bluestem. In order to capture this difference, we choose colonization parameters $c_1 = 1.0 \text{ years}^{-1}$ for big bluestem and $c_2 = 5.0 \text{ years}^{-1}$ for milkweed. For the mortality parameters, we let $m_1 = m_2 = 0.5 \text{ years}^{-1}$. Although these precise parameter values are somewhat arbitrary, from a qualitative perspective, this scenario does capture the colonization-competition trade-off of these two common grassland species.

Beyond these rough estimates for c_1 , c_2 , m_1 , and m_2 , the only parameters left to estimate are the seed retention factors f_1 and f_2 . We will compute the seed retention factors exactly as described in section 2.3. First, each species' dispersal kernel must be determined. For this example, we will assume that both species have bivariate normal dispersal kernels. A "fat tailed" distribution like the inverse Gaussian or Laplace distribution, or even an asymmetric distribution (to account for prevailing winds) may be more realistic, but for the sake of simplicity, we consider only the bivariate normal distribution:

$$g(x, y) = \frac{1}{2\pi\sigma^2} \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right).$$

The standard deviation σ should be larger for species whose seeds travel longer distances and smaller for species whose seeds travel shorter distances. Since milkweed's seeds

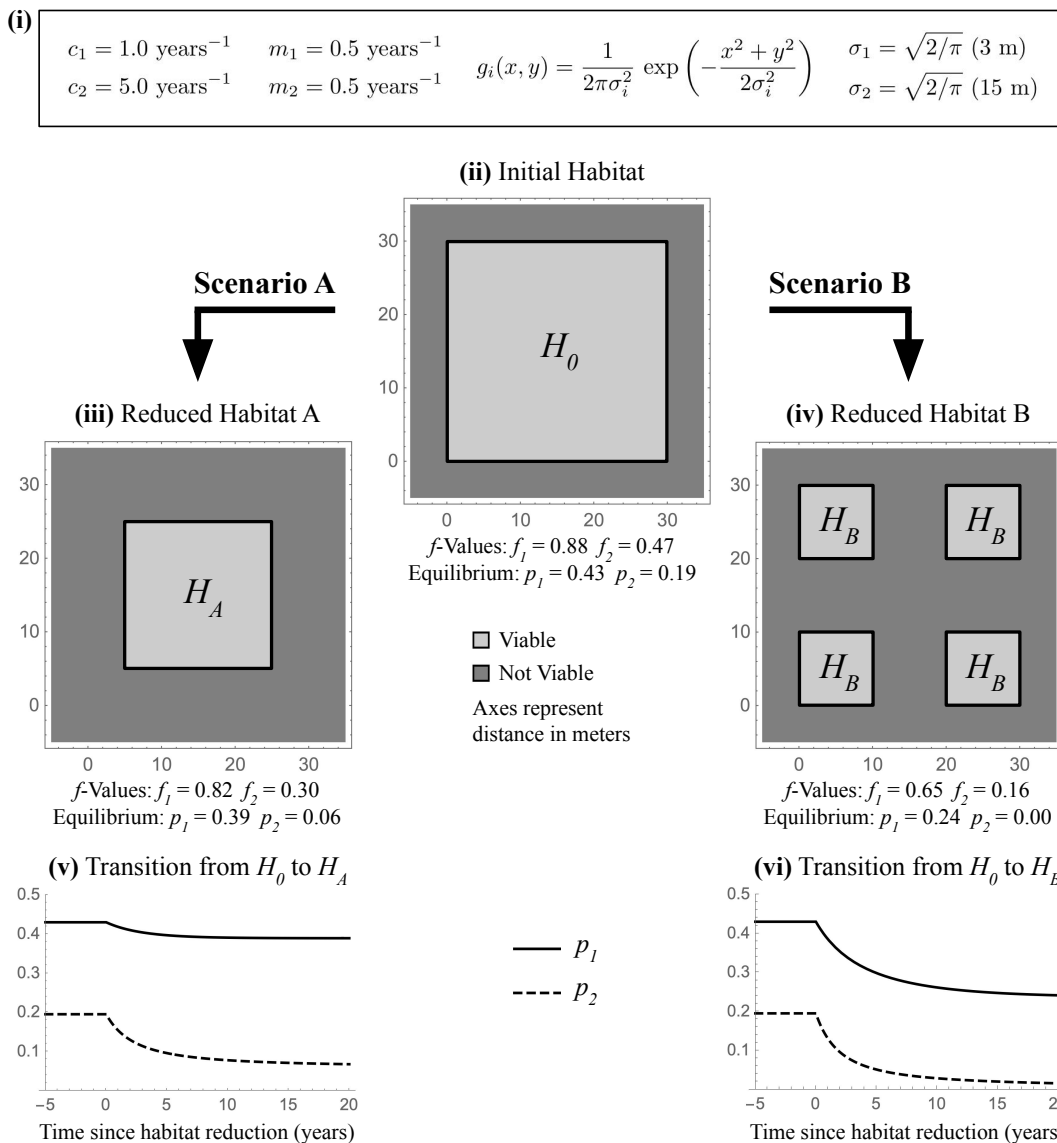


Figure 4: In this 2-species example, the model parameters shown in panel (i) are chosen to approximate the traits of big bluestem (species 1) and common milkweed (species 2). Three different habitat geometries, H_0 , H_A , and H_B , are shown in panels (ii), (iii), and (iv). Initially, the two plant populations occupy H_0 in a stable equilibrium ($p_1 = 0.43$, $p_2 = 0.19$). Then, at $t = 0$, the viable habitat is reduced from H_0 to either H_A or H_B in Scenario A or B respectively. The resulting decrease in seed retention factors causes the plant populations to decline to reduced equilibria, as shown in panels (v) and (vi). Note that the same percentage of habitat area is destroyed in both scenarios, but the consequences are more severe in scenario B, where milkweed will eventually go extinct.

are very light and have parachute-like plumes to catch the wind, they tend to travel much farther than big bluestem's heavier plume-less seeds. Qualitatively, it follows that $\sigma_1 < \sigma_2$. To quantify this, we turn to a 2018 mechanistic seed dispersal study, which estimated mean seed dispersal distances of several common grassland plant species [7]. Based on average seed mass, terminal velocity, release height, and wind conditions at the typical release date, [7] predicts mean seed dispersal distances of roughly $\mu_1 = 3$ m and $\mu_2 = 15$ m for big bluestem and common milkweed, respectively. Using the relation $\mu = \sqrt{\pi/2}\sigma$ (see Appendix II for derivation), we conclude that

$$\begin{aligned}\sigma_1 &= \sqrt{2/\pi}(3 \text{ m}) \approx 2.4 \text{ m} \\ \sigma_2 &= \sqrt{2/\pi}(15 \text{ m}) \approx 12 \text{ m}.\end{aligned}$$

The parameters mentioned so far (colonization rates, mortality rates, and dispersal kernels) are summarized in panel (i) of Figure 4. All that remains to define is the habitat geometry H . We begin with a small 30 m square of area 900 m², shown in panel (ii), which we call H_0 . We then consider two hypothetical habitat destruction scenarios. In panel (iii), the outermost 5 m along each of the square's edges is destroyed, leaving a 20 m square, H_A . In panel (iv), a cross shape is destroyed, fragmenting the habitat into four isolated 10 m squares, H_B . These scenarios could represent the construction of new roads, the expansion of agricultural fields, or some other sudden reduction in viable habitat. Note that in both scenarios, 500 m² are destroyed, leaving a reduced habitat of area 400 m². We juxtapose these two scenarios in order to demonstrate the importance of habitat geometry, not just total habitat area, for species population dynamics after destruction.

Numerically computing the seed retention factors using equation (5) yields lower f -values in H_A and H_B than in H_0 for both big bluestem and milkweed, as expected from habitat destruction. But, there is a significant difference between H_A and H_B , despite their equal area. In H_A , big bluestem and milkweed's f -values are 0.82 and 0.30, respectively, while in H_B they are 0.65 and 0.16. As a result of these lower seed retention factors, the transition from H_0 to H_B in scenario B causes a more severe decline in plant populations than the transition from H_0 to H_A in scenario A. In scenario A, both species survive at reduced equilibrium populations, whereas in scenario B, only big bluestem survives. Milkweed's equilibrium population in scenario B is zero, so the species suffers what Tilman calls an "extinction debt," meaning its population will deterministically decline to zero barring further intervention, shown in panel (vi) of Figure 4. This example demonstrates that the geometry of the habitat, not just its area, can be decisive for population viability.

We conclude that small and fragmented habitats like H_B make species more vulnerable to seed loss, putting them at greater risk of extinction. In general, we found that continuous habitats with minimal edge length retained the most seeds and resulted in the fewest extinctions.

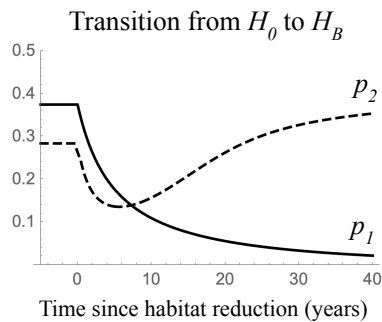


Figure 5: Revisiting the illustrative example from section 3, we increase the mean dispersal distance of big bluestem (species 1) from 3 meters to 5 meters while holding all other parameters constant. Big bluestem's seed retention factor drops from 0.65 to 0.47 in H_B and its population crashes, leaving room for milkweed's population to rebound. Comparing panel (vi) of Figure 2 with the model's new prediction above shows a drastic reversal.

We also noticed that even small changes in dispersal distance can significantly affect the predicted outcome. For instance, increasing the mean dispersal distance of big bluestem from 3 meters to 5 meters while holding all other parameters constant leads to drastically different behavior in Scenario B. This change reduces big bluestem's seed retention factor from 0.65 to 0.47 in habitat H_B , pushing it to extinction and leaving room for milkweed to make a dramatic comeback, as shown in Figure 5. In Scenario A, big bluestem's seed retention factor changes from 0.82 to 0.71 and both species persist on the landscape, as before.

4 Discussion

The example in section 3 illustrates another prediction of the seed-loss model about which species are most vulnerable after habitat destruction. Specifically, the model predicts that species whose seeds travel the farthest are most prone to seed loss. For instance, in the example in section 3, milkweed has a lower seed retention factor than big bluestem in all three habitats because its larger dispersal kernel results in more seeds landing outside the viable habitat. Species like milkweed with larger dispersal kernels tend to be on the colonization side of the competition-colonization trade-off, so the seed-loss model generally predicts that the best colonizers are most prone to seed loss after habitat destruction. However, this does not necessarily mean the best colonizer always goes extinct first, since the population of each species depends not just on its seed retention factor but also on colonization, mortality, and competitive interactions with other species in the model. In some cases the best colonizer goes extinct (see Figure 4), in other cases the best competitor goes extinct (see Figure 5), and in still other cases

multiple species or a species in the middle of the colonization-competition spectrum go extinct.

These results differ significantly from the predictions of the Tilman model. In the Tilman model, the first species to go extinct as the habitat destruction parameter D is increased is always the best competitor, species 1. Furthermore, Tilman predicts that the critical value of D beyond which species 1 goes extinct is always $D = 1 - m_1/c_1$, which also happens to be species 1's equilibrium population when $D = 0$ [9]. The seed-loss model, in contrast, is less sensitive to the exact percentage of habitat area destroyed and more sensitive to the geometry and scale of the habitat, which interacts with the geometry and scale of each species' dispersal kernel. This difference between the seed-loss model and the Tilman model is due to the spatially explicit computation of seed retention factors, which allows the ordinary differential equations (4) to capture some of the two dimensional dynamics of seed dispersal while remaining spatially implicit.

This two dimensional geometric interaction between habitat and dispersal kernel, specifically the ratio of dispersal distance to habitat size, has also emerged as a key predictor of species extinction in spatially explicit models of plant population dynamics, including a Markov model of colonization and competition on an integer lattice [6] as well as a single-species PDE on a one-dimensional habitat [3].

Several simplifying assumptions in the seed-loss model could be revisited for greater realism. The seed-loss model assumes that the sole mechanism for plant reproduction is seed dispersal. However, vegetative reproduction is especially common among grassland plants. The seed-loss model also assumes that seeds disperse only by wind, which ignores the impacts of insects, animals, and humans as seed dispersers. Another simplifying assumption, mentioned in section 2.3, is that plants are evenly distributed throughout the habitat. A more realistic model might allow for some species to prefer the middle of the habitat, others to prefer the edges, and still others to prefer the upwind, downwind, north, or south sides. Finally, precise estimation of colonization and mortality parameters is quite difficult. For example, it is not clear exactly how plants die, or how to classify a plant as dead, particularly in the case of vegetative plants. Because of this, the seed-loss model is more valuable as a qualitative tool than a quantitative one.

Despite these limitations, spatially implicit ODE models such as the seed-loss model have an advantage in their simplicity and analytic tractability. This can allow the same qualitative insights as more complex models through much simpler calculations of equilibria. The seed-loss model has already produced qualitatively supported results [3, 6] that are relevant to conservation strategies and we are excited to continue to explore more habitat geometries and analyze intervention strategies like reseeded or habitat restoration.

5 Conclusion

In this paper we introduce the seed-loss model, which accounts for seed loss in small and fragmented habitats. We do this by introducing a seed retention parameter f , which denotes the fraction of a plant species' seeds that land within viable habitat. Given the spatial dispersal pattern of a species' seeds and the geometry of a habitat, the seed-loss model can predict species dynamics and deterministic extinction. One interesting implication of the seed-loss model is that it is no longer straightforward which species will go extinct first in a habitat with multiple species. Extinction depends on the dispersal kernel of each species and the specific geometry of the given habitat. The seed-loss model can be used to give a nuanced, qualitative picture of what is possible when it comes to habitat destruction, biodiversity loss, and attempts to mitigate deterministic extinction of plant species.

6 Appendix I

Here we show that the seed-loss model is equivalent to the Tilman model with the substitution $f = 1 - D$ and a re-scaling of p in the one-species case. For clarity, we denote the plant population variable as \hat{p} for the Tilman model and as p for the seed-loss model. We begin with the Tilman model

$$\frac{d\hat{p}}{dt} = c\hat{p}(1 - D - \hat{p}) - m\hat{p} \quad (6)$$

and then make the substitution $\hat{p} = p(1 - D)$. Concretely, \hat{p} represents the occupied sites as a fraction of total habitat (viable and destroyed), whereas p represents the occupied sites as a fraction of only the viable habitat. With this change of variables, (6) becomes

$$\begin{aligned} \frac{d((1 - D)p)}{dt} &= c(1 - D)p(1 - D - (1 - D)p) - m(1 - D)p \\ (1 - D)\frac{dp}{dt} &= cp(1 - D)^2(1 - p) - m(1 - D)p \\ \frac{dp}{dt} &= cp(1 - D)(1 - p) - mp. \end{aligned}$$

Finally, we can substitute $f = (1 - D)$ to obtain the seed-loss model

$$\frac{dp}{dt} = cf p(1 - p) - mp$$

as claimed.

The same substitution works in the multi-species case, with the important caveat that all species must have equal seed retention factors f_i . Consider the differential

equation for species i in the multi-species Tilman model

$$\frac{d\hat{p}_i}{dt} = c_i \hat{p}_i \left(1 - D - \sum_{j=1}^i \hat{p}_j\right) - m_i \hat{p}_i - \sum_{j=1}^{i-1} c_j \hat{p}_j \hat{p}_i$$

with the substitution $\hat{p}_i = p_i(1 - D)$.

$$\frac{d(p_i(1 - D))}{dt} = c_i p_i(1 - D) \left(1 - D - \sum_{j=1}^i p_j(1 - D)\right) - m_i p_i(1 - D) - \sum_{j=1}^{i-1} c_j p_j(1 - D) p_i(1 - D)$$

$$(1 - D) \frac{dp_i}{dt} = c_i p_i(1 - D) \left(1 - D - (1 - D) \sum_{j=1}^i p_j\right) - m_i p_i(1 - D) - (1 - D) \sum_{j=1}^{i-1} c_j p_j p_i(1 - D)$$

$$\frac{dp_i}{dt} = c_i p_i \left(1 - D - (1 - D) \sum_{j=1}^i p_j\right) - m_i p_i - \sum_{j=1}^{i-1} c_j p_j p_i(1 - D)$$

$$\frac{dp_i}{dt} = (1 - D) c_i p_i \left(1 - \sum_{j=1}^i p_j\right) - m_i p_i - \sum_{j=1}^{i-1} c_j p_j p_i(1 - D)$$

At this point, the equality of the seed retention factors is required in order to make the substitution $f = (1 - D)$, resulting in

$$\frac{dp_i}{dt} = c_i f p_i \left(1 - \sum_{j=1}^i p_j\right) - m_i p_i - \sum_{j=1}^{i-1} c_j f p_j p_i$$

as desired.

7 Appendix II

In section 3, we claimed that the mean distance from the origin of the bivariate normal distribution

$$g(x, y) = \frac{1}{2\pi\sigma^2} \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right)$$

is $\mu = \sqrt{\pi/2}\sigma$. To show this is true, it suffices to evaluate the integral

$$\mu = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} g(x, y) \sqrt{x^2 + y^2} dx dy.$$

Substituting the bivariate normal function for $g(x, y)$ and switching to polar coordinates yields

$$\begin{aligned} \mu &= \int_0^{2\pi} \int_0^{\infty} \frac{1}{2\pi\sigma^2} e^{-r^2/2\sigma^2} r^2 dr d\theta \\ \mu &= \int_0^{\infty} \frac{1}{\sigma^2} e^{-r^2/2\sigma^2} r^2 dr. \end{aligned}$$

Now change variables to $t = r/(\sqrt{2}\sigma)$, yielding

$$\mu = \int_0^\infty 2\sqrt{2}\sigma e^{-t^2} t^2 dt$$

and integrate by parts with $u = \sqrt{2}\sigma t$ and $dv = 2te^{-t^2} dt$. This means $du = \sqrt{2}\sigma dt$ and $v = -e^{-t^2}$. The result is

$$\mu = (\sqrt{2}\sigma t)(-e^{-t^2}) \Big|_{t=0}^{t=\infty} - \int_0^\infty (-e^{-t^2})(\sqrt{2}\sigma dt)$$

The first term vanishes at both $t = 0$ and $t = \infty$, leaving only

$$\mu = \sqrt{2}\sigma \int_0^\infty e^{-t^2} dt.$$

This integral is exactly half of the famous Gaussian integral

$$\int_{-\infty}^\infty e^{-t^2} dt = \sqrt{\pi}$$

so we have

$$\mu = \sqrt{2}\sigma \frac{\sqrt{\pi}}{2} = \sqrt{\pi/2}\sigma$$

as claimed.

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