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Effects of Forest Spatial Structure on Insect Outbreaks: Insights from a Host-Parasitoid Model

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ABSTRACT: Understanding how cycles of forest-defoliating insects are affected by forest destruction is of major importance for forest management. Achieving such an understanding with data alone is difficult, however, because population cycles are typically driven by species interactions that are highly nonlinear. We therefore constructed a mathematical model to investigate the effects of forest destruction on defoliator cycles, focusing on defoliator cycles driven by parasitoids. Our model shows that forest destruction can increase defoliator density when parasitoids disperse much farther than defoliators because the benefits of reduced defoliator mortality due to increased parasitoid dispersal mortality exceed the costs of increased defoliator dispersal mortality. This novel result can explain observations of increased outbreak duration with increasing forest fragmentation in forest tent caterpillar populations. Our model also shows that larger habitat patches can mitigate habitat loss, with clear implications for forest management. To better understand our results, we developed an approximate model that shows that defoliator spatial dynamics can be predicted from the proportion of dispersing animals that land in suitable habitat. This approximate model is practically useful because its parameters can be estimated from widely available data. Our model thus suggests that forest destruction may exacerbate defoliator outbreaks but that management practices could mitigate such effects.

Keywords: forest fragmentation, dispersal success approximation, Malacosoma disstria, functional landscape connectivity, insect outbreaks, host-parasitoid.

Introduction

Periodic outbreaks of forest insects kill trees and can contribute to global climate change (Malmstrom and Raffa 2000; Kurz et al. 2008; Galik and Jackson 2009; McDow-

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ell et al. 2011), while human activities alter the amount of forest and change the size of forest patches (Neigh et al. 2008; Frolking et al. 2009; Rhemtulla et al. 2009). Sustainable forest management thus requires an understanding of how outbreaks interact with human activities and other forest disturbances (Malmstrom and Raffa 2000; Folke et al. 2004; Perry and Enright 2006; Galik and Jackson 2009; Seidl et al. 2011). In this article, we use a mathematical model to investigate the effects of changing forest landscape structure on insect outbreaks that are driven by host-parasitoid interactions. Previous spatially explicit host-parasitoid and predator-prey models have shown that both habitat patch size and distances between patches can alter population density (Cronin and Reeve 2005; Murrell 2005; Johnson et al. 2006; Hirzel et al. 2007; Reeve et al. 2008; Strohm and Tyson 2009; Su et al. 2009). Existing models of forest insect population dynamics, however, are mostly nonspatial (Turchin 2003; Turchin et al. 2003; Dwyer et al. 2004; Cobbold et al. 2009) or include space in very simple and hence unrealistic ways (Cobbold et al. 2005; Johnson et al. 2006; Hirzel et al. 2007; Strohm and Tyson 2009; Su et al. 2009). We therefore extend a simple insect-parasitoid model to allow for complex spatial patterns of forest habitat, hereafter referred to as landscape configuration, to understand how forest destruction and consequent changes in the size and arrangement of forest patches affect insect outbreaks.

We focus on the forest tent caterpillar (FTC; *Malacosoma disstria* Hubner). Previous researchers have developed a nonspatial model that provides an accurate description of local temporal dynamics (Cobbold et al. 2005, 2009), thus providing a well-supported starting point for our investigations of spatial dynamics. We simulate model dynamics on complex, patchy landscapes that vary in the amount and aggregation of habitat to show that the effect of habitat loss depends on the relative dispersal abilities of herbivores and parasitoids and on the arrangement of

habitat. When habitat is scarce and dispersal distances are intermediate, increasing spatial autocorrelation or habitat patch size in our model can reduce the effects of habitat loss, a result consistent with previous results of both theoretical (North and Ovaskainen 2007) and empirical (Andrén 1994; Swift and Hannon 2010) studies.

Previous models of spatial host-parasitoid dynamics, however, have neglected the effects of mortality due to dispersal into unsuitable habitats. Such models therefore predict that habitat loss will benefit herbivores when parasitoids are less mobile than herbivores (Ryall and Fahrig 2006; Holt and Barfield 2009). Because our model does account for dispersal into unsuitable habitats, it instead predicts that habitat loss will benefit herbivores when parasitoids are more mobile than herbivores. Moreover, because of the effects of habitat loss on parasitoids, our model predicts that increased habitat loss can also lead to increased outbreak duration, a result that matches data showing that FTC outbreaks last longer as habitat loss increases (Roland 1993; Roland and Taylor 1995, 1997; Roland et al. 1998; Rothman and Roland 1998; Cooke and Roland 2000; Roth et al. 2006). Our model thus provides a simple mechanistic explanation for an important pattern observed in the field, thereby demonstrating the utility of mechanistic spatial models for understanding large-scale ecological data sets. We also present an approximate model that shows that the results of our more realistic model can largely be predicted from the fraction of hosts and parasitoids that disperse successfully at each location. This local dispersal success approximation is useful because it emphasizes that the effects of landscape configuration are caused by dispersal mortality and because its parameters can be estimated from widely available habitat distribution data. Local dispersal success is essentially a patch-based measure of potential functional connectivity (Kindlmann and Burel 2008) that quantifies in our model "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993, p. 571). Although our work suggests that the effects of forest destruction on insect outbreaks are complex, the local dispersal success approximation may provide a way of predicting such effects from easily collected data.

Spatial Population Model

Model Structure

FTCs have a univoltine life cycle, in which there is a single generation per year (Fitzgerald 1995). Damage to host trees is caused by larvae feeding on buds and foliage in the spring and early summer. Most mortality from parasitoids occurs in the larval and pupal stages. Adults disperse in late summer and fall but do not feed on or cause damage to their host

trees. A natural choice for this species is thus a discrete-time model with an annual time step in which birth, density-dependent mortality, and dispersal occur in sequence (Cobbold et al. 2005, 2009). Because we are mainly concerned with understanding and predicting defoliation caused by larvae, our model tracks the population density of late larval stages before metamorphosis and dispersal, meaning that growth occurs after dispersal.

A range of evidence suggests that FTC outbreaks are driven by interactions with specialist parasitoids (Cobbold et al. 2005, 2009). Adding dispersal to a discrete-time host-parasitoid model then gives a spatially discretized integro-difference model:

$$
\begin{aligned}
\underbrace{H_{i,t+1}}_{\text{herbivores}} &= \underbrace{h(H_{i,t}^*, P_{i,t}^*)}_{\text{growth}}, \\[2ex]
\underbrace{H_{i,t}^*}_{\text{herbivores after dispersal}} &= \sum_{j=1}^{\Omega} \underbrace{k(d_{i,j}, \bar{d}_{\mathrm{H}})}_{\text{dispersal kernal}} H_{j,t}, \\[2ex]
\underbrace{P_{i,t+1}}_{\text{parasitoids}} &= \underbrace{g(H_{i,t}^*, P_{i,t}^*)}_{\text{growth}}, \\[2ex]
\underbrace{P_{i,t}^*}_{\text{parasitoids after dispersal}} &= \sum_{j=1}^{\Omega} \underbrace{k(d_{i,j}, \bar{d}_{P})}_{\text{dispersal kernel}} P_{j,t}.
\end{aligned}
\tag{1}
$$

The parameters $H_{i,t}$ and $P_{i,t}$ are herbivore and parasitoid densities after growth and before dispersal in year t at location i in the spatial domain Ω, which represents the landscape, while $H_{i,t}^*$ and $P_{i,t}^*$ are herbivore and parasitoid population densities after dispersal. The probability of dispersing from location j to location i, as described by the dispersal kernel $k(., .)$, depends only on the distance between i and j ($d_{i,j}$), but the mean dispersal distances, $\bar{d}_{\mathrm{H}}$ and $\bar{d}_{\mathrm{P}}$, can differ between herbivores ($H_{i,t}$) and parasitoids ($P_{i,t}$). The functions $h(.)$ and $g(.)$ then determine the local population dynamics of herbivores and parasitoids. Animals die if they disperse to areas where the population growth rate is 0, and we therefore refer to areas that allow population growth as "suitable habitat."

To describe local population dynamics, we use a model developed by Cobbold et al. (2005, 2009) that explains important patterns in long-term data:

$$
\begin{aligned}
h(H_{i,t}^*, P_{i,t}^*) &= I_i \lambda H_{i,t}^* e^{-\log(\lambda) H_{i,t}^*} e^{-P_{i,t}^*}, \\[2ex]
g(H_{i,t}^*, P_{i,t}^*) &= I_i \xi H_{i,t}^* (1 - e^{-P_{i,t}^*}) e^{-\varphi \log(\lambda) H_{i,t}^*}.
\end{aligned}
\tag{2}
$$

The parameter I_i indicates habitat suitability (1 is suitable, 0 otherwise). In the absence of parasitoids, this is a Ricker model (Ricker 1954) with intrinsic growth rate for herbivores λ. To reduce the number of model parameters, we use a dimensionless version of the model in which herbi-

vore density is expressed as a proportion of herbivore carrying capacity K; see Cobbold et al. (2005) for details. We therefore write $H_{i,t}^* = h_{i,t}/K$, where $h_{i,t}$ is the unscaled herbivore density after dispersal, so that $H_{i,t}^*$ varies between 0 and 1. Similarly, parasitoid density is scaled by the search rate, such that $P_{i,t}^* = p_{i,t}a$, where $P_{i,t}^*$ is the nondimensional parasitoid density, $p_{i,t}$ is the unscaled parasitoid density, and a is the parasitoid search rate. The parameter ξ thus depends on the parasitoid search rate, the parasitoid growth rate, and the herbivore carrying capacity according to $\xi = abK$, where b is the number of parasitoids produced per parasitized herbivore (Jang and Johnson 2009).

Parasitoid population density is modified by the density-dependent mortality of herbivores, to reflect the fact that the death of an herbivore may kill the parasitoid developing within. In particular, φ determines parasitoid phenology, such that $\varphi = 0$ means that parasitoids emerge before density-dependent mortality of herbivores, while $\varphi = 1$ means that parasitoids emerge after density-dependent mortality. Setting $\varphi > 0$ thus imposes density-dependent mortality on parasitoids. Otherwise, the model is a standard Beddington model with a linear parasitoid functional response (Beddington et al. 1976; Turchin 2003).

Cobbold et al. (2009) constructed this model by using a combination of experimental and observation data for the FTC to choose among different possible functional forms of important model components. First, they used experimental data to choose among competing models of herbivore density dependence, showing that the data are best explained by a Ricker function. Second, they used observational data to show that the Nicholson-Bailey parasitism model of attack rates, which is based on a Poisson distribution (Nicholson and Bailey 1935), provides a more parsimonious fit to parasitism rates in the field than does the Hassell-May model, which is based on a negative binomial distribution. Finally, they used data on the timing of outbreaks to estimate the density-dependence parameter φ. The model based on these functional forms and parameter estimates shows long-period, large-amplitude fluctuations in host density that match the period and amplitude of outbreaks observed in nature. This empirical support for the model suggests that it provides a useful description of how parasitoids drive FTC outbreaks.

Dispersal Kernel

For most forest insects, including the FTC, there are few data on dispersal distances, dispersal kernel shapes, emigration rates, and other aspects of dispersal behavior (Greenbank et al. 1980; Safranyik et al. 1992; Baltensweiler and Rubli 1999; Cobbold et al. 2005) and even less knowledge of parasitoid dispersal (Godfray 1994; Mondor and Roland 1997, 1998; Roland and Taylor 1997; Cappuccino

et al. 1998; Rothman and Roland 1998; Hastings 2000; Cobbold et al. 2005; Roth et al. 2006; Babin-Fenske and Anand 2011). We therefore use very simple dispersal kernels. In our model, herbivores and parasitoids disperse independently of one another, and for each animal the probability of moving from location i to location j depends only on the distance between locations. The dispersal kernel that we used is

$$\underbrace{k(d_{i,j}, \bar{d}_x)}_{\text{dispersal kernel}} = \begin{cases} 0 & \text{if } d_{i,j} > d_{\max}, \\ \dfrac{m(d_{i,j}, \bar{d}_x)(\Delta x)^2}{\displaystyle\sum_{j:d_{i,j} \leq d_{\max}} m(d_{i,j}, \bar{d}_x)(\Delta x)^2} & \text{otherwise,} \end{cases} \tag{3}$$

$$\text{where } m(d_{i,j}, \bar{d}_x) = \frac{2}{\pi \bar{d}_x^2} e^{-2d_{i,j}/\bar{d}_x}$$

$$\text{and } d_{\max} = -0.5\bar{d}_x \log(\pi \bar{d}_x^2 10^{-10}/2).$$

Here, $d_{i,j}$ is the Euclidean distance between the center points of grid cells i and j, and $(\Delta x)^2 = 0.01 \text{ km}^2$ is the area of one grid cell. The average dispersal distance ($\bar{d}_x$) is allowed to differ between herbivores ($x = H$) and parasitoids ($x = P$). The dispersal kernel $k(d_{i,j}, \bar{d}_x)$ is thus based on an exponential dispersal function $m(d_{i,j}, \bar{d}_x)$ (Clark et al. 1999) describing the proportion of animals dispersing a distance $d_{i,j}$. Because our model uses discrete space, we discretized $m(d_{i,j}, \bar{d}_x)$ by centering and standardized it to ensure that herbivores and parasitoids were not lost to discretization. To speed computation, we assumed that dispersal probabilities of less than 10^{-10} were negligible (Abbott and Dwyer 2008), so that there is no dispersal beyond the maximum dispersal distance of $d_{\max}$. We then used a discrete fast Fourier transform with absorbing boundary conditions (fftconvolve function in Jones et al. 2001) to carry out the dispersal calculations.

Landscape Configuration

To investigate the effect of variation in the statistical properties of landscapes, we generated landscapes from a stochastic process defined by a spatial covariance function and by the proportion of landscape f that is suitable habitat (Keitt 2000; Fortin et al. 2003; Diggle and Ribeiro 2006; James et al. 2011). This method generates patchy landscapes similar to those found in nature and allows us to distinguish between the effects of habitat loss and habitat arrangement (Andrén 1994; Fahrig 2003). The method also allows us to draw conclusions about sets of landscapes with similar statistical properties caused by similar generating processes rather than about particular landscapes.

The FTC literature generally uses the term "fragmentation" to refer both to habitat loss and to changes in habitat arrangement (Roland 1993, 2005; Roland and Taylor 1997;

Rothman and Roland 1998; Cooke and Roland 2000; Wood et al. 2010). To avoid confusion with this literature, we refer to changes in habitat configuration that are independent of habitat loss as "habitat arrangement" instead of "fragmentation per se," as used in the influential review of Fahrig (2003). We then assumed that the spatial autocorrelation in habitat suitability declines exponentially with the distance between locations, so that the covariance equals $e^{-d_{i,j}/\alpha}$ if $\alpha > 0$ and 0 otherwise. The spatial covariance is thus equal to 0.5 if $d_{i,j} = \log(2)\alpha$, emphasizing that α determines the extent of spatial autocorrelation and thus the habitat arrangement.

We then generated autocorrelated landscapes using Gaussian random fields (Schlather 2001; Diggle and Ribeiro 2006; James et al. 2011). To construct binary landscapes, such that a proportion f of grid cells are suitable habitat, we applied a threshold to each Gaussian random field, designating the highest values as suitable habitat and all other areas as unsuitable habitat (fig. 1). Each cell (pixel or location) is 0.1 km wide and landscapes are 10 km × 10 km, so there are 10,000 cells per landscape.

Parameter Values

To understand how the effects of landscape configuration depend on parameters governing local population dynamics and dispersal, we varied the dispersal parameters $\bar{d}_H$ and $\bar{d}_P$ over reasonable ranges. The work of Cobbold et al. (2009) provides demographic parameter estimates, but because we are interested in general patterns, we also consider broader ranges of these demographic parameters.

The herbivore reproductive rate λ was constrained to focus attention on cyclic population dynamics because cycles best match the dynamics observed in the field. We therefore assumed $1 \leq \lambda \leq e^2$, which ensured that herbivores in the nonspatial model would approach a stable nonzero equilibrium in the absence of parasitoids (app. A). Parameter ranges are shown in table 1, and their effects on nonspatial model behavior are shown in appendix C (apps. C and D are available online). For each combination of parameter values, we then generated a binary 10 × 10-km landscape consisting of 10,000 cells or locations, and we simulated model dynamics for 1,000 years. A total of 162,000 combinations of parameter values were thus used for the model.

In nature, the scale of forest patchiness varies widely, from tens of meters to hundreds of kilometers, depending on patterns of fire, logging, wind, insects, and other disturbances (Vepakomma et al. 2010; James et al. 2011). Meanwhile, realistic average dispersal distances for most forest defoliators and their parasitoids are less than 2 km. For insects with such short dispersal distances, there is little difference between forest patches of 10 km² and 100 km². Moreover, for a given grid resolution, computational costs increase with increasing landscape size, which is important because the computational costs of exploring a reasonable parameter space were almost prohibitive. We therefore
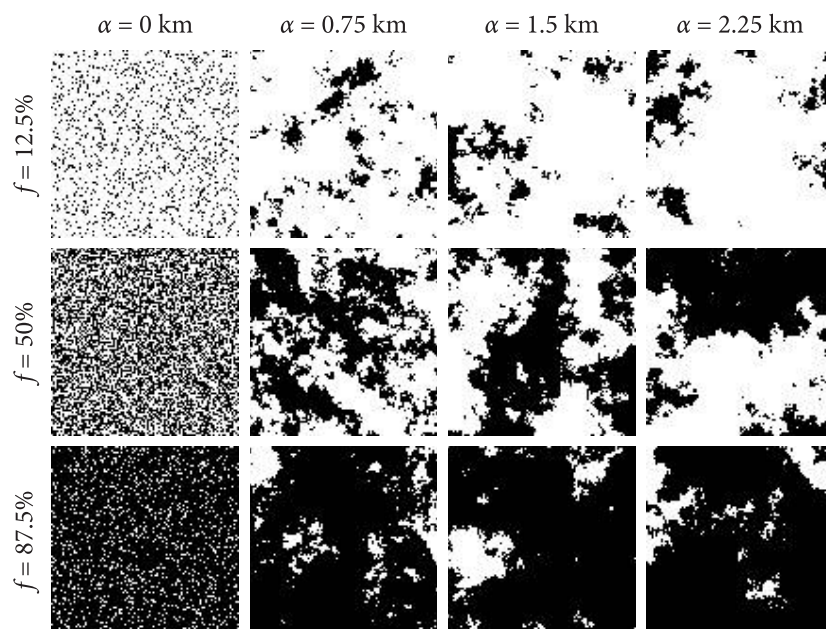

Figure 1: Example landscapes. Black indicates suitable habitat, and white indicates unsuitable habitat where insects cannot reproduce. Habitat arrangement α varies from left to right, and habitat amount f varies from top to bottom.

Table 1: Model parameter values

Symbol	Description	Value
Base parameters:		
D	Grid cell width	.1 km
A	Grid cell area	.01 km^2
Ω	Size of the domain	10,000 cells
Ω_{rows}	Number of rows	100 cells
Ω_{cols}	Number of columns	100 cells
T	Maximum time	1,000 years
b	Burn-in period	800 years
Local population dynamics:		
λ	H growth rate	1.5, 3, 5, 7 (**2.61**)
ξ	P growth rate	1, 5, 10, 30, 50 (**8.06**)
φ	P phenology	0, .25, .50, .75, 1 (**.35**)
Dispersal:		
$\bar{d}_H$	H dispersal distance	.1, .4, .7, 1 (**1**) km
$\bar{d}_P$	P dispersal distance	.1, .4, .7, 1, 1.3 (**.4**) km
Landscape configuration:		
f	Habitat amount	.0001, .125, .25, .375, .5, .625, .75, .875, 1
α	Habitat arrangement	0, .375, .75, 1.125, 1.5, 1.875, 2.25, 2.625, 3 km
Initial conditions:		
$H_{i,0}$	Initial H density	$U(.99, 1.01)\hat{H}$
$P_{i,0}$	Initial P density	$U(.99, 1.01)\hat{P}$

Note: Parameters governing local dynamics (λ, ξ, and φ), dispersal distance ($\bar{d}_H$ and $\bar{d}_P$), and landscape configuration (f and α) were varied in a factorial experimental design. Baseline parameter values are shown in boldface type (Cobbold et al. 2005, 2009). $U(0.99, 1.01)$ indicates random values from a uniform distribution between 0.99 and 1.01, and $\hat{H}$ and $\hat{P}$ are equilibrium densities in the nonspatial model (app. A). The first b years of each simulation were discarded as transients.

considered landscapes of 10 km^2 containing patches of size 10 km^2 or less (fig. 1). To further reduce computational costs, we assumed that landscape structure was the only source of stochasticity in our model. Stochasticity often has only slight effects on the large-amplitude, long-period limit cycles that we are most interested in (Dwyer et al. 2004), so our results are likely to be robust to this omission.

As we will show, in some cases parasitoids effectively become extinct even though the local dispersal success approximation predicts that parasitoids should be able to invade the host population (app. A). Extinction occurs in such cases because high parasitoid growth rates (ξ) lead to large amplitude population fluctuations that drive parasitoid population densities below the smallest number that can be stored by the computer, so that coexistence of hosts and parasitoids is effectively impossible (as in Beddington et al. 1976). We omitted such cases from further consideration because parasitoids and herbivores clearly do coexist in the FTC system.

Effects of Landscape Configuration on Herbivore Density

In forest management, a primary concern is how much damage insects will cause to trees, a problem that increases in severity with increasing herbivore population density (Roland 2005). The statistic of interest is therefore the aver-

age herbivore population density ($\overline{H}$) in suitable habitat patches. To eliminate transients, we calculated mean herbivore density ($\overline{H}$) in suitable habitat over the final 200 years of each 1,000-year simulation:

$$\overline{H} = \frac{1}{f\Omega 200} \sum_{t=801}^{1,000} \sum_{i=1}^{\Omega} H_{i,t}. \tag{4}$$

Here, Ω is the number of pixels in each landscape, and $f\Omega$ is the number of pixels that are suitable habitat. In landscapes that contained more than 100 suitable habitat cells, we calculated mean herbivore density over 100 randomly selected suitable locations, so that at least 1% of the landscape cells were analyzed. We subsampled in this manner to limit storage requirements and computing time. This was necessary because 100 locations per landscape, 200 years per landscape, and 162,000 combinations of model parameter values gave us 3.24×10^9 records of herbivore population density.

The model shows that in some cases it is possible for loss of habitat to lead to increased herbivore density. The most interesting case is when the model shows cycles corresponding to realistic population dynamics, as in figures 2 and 3a. In this case, loss of habitat leads to increased herbivore density for the lowest herbivore dispersal distance ($\bar{d}_H = 0.1$ km) in combination with the intermediate
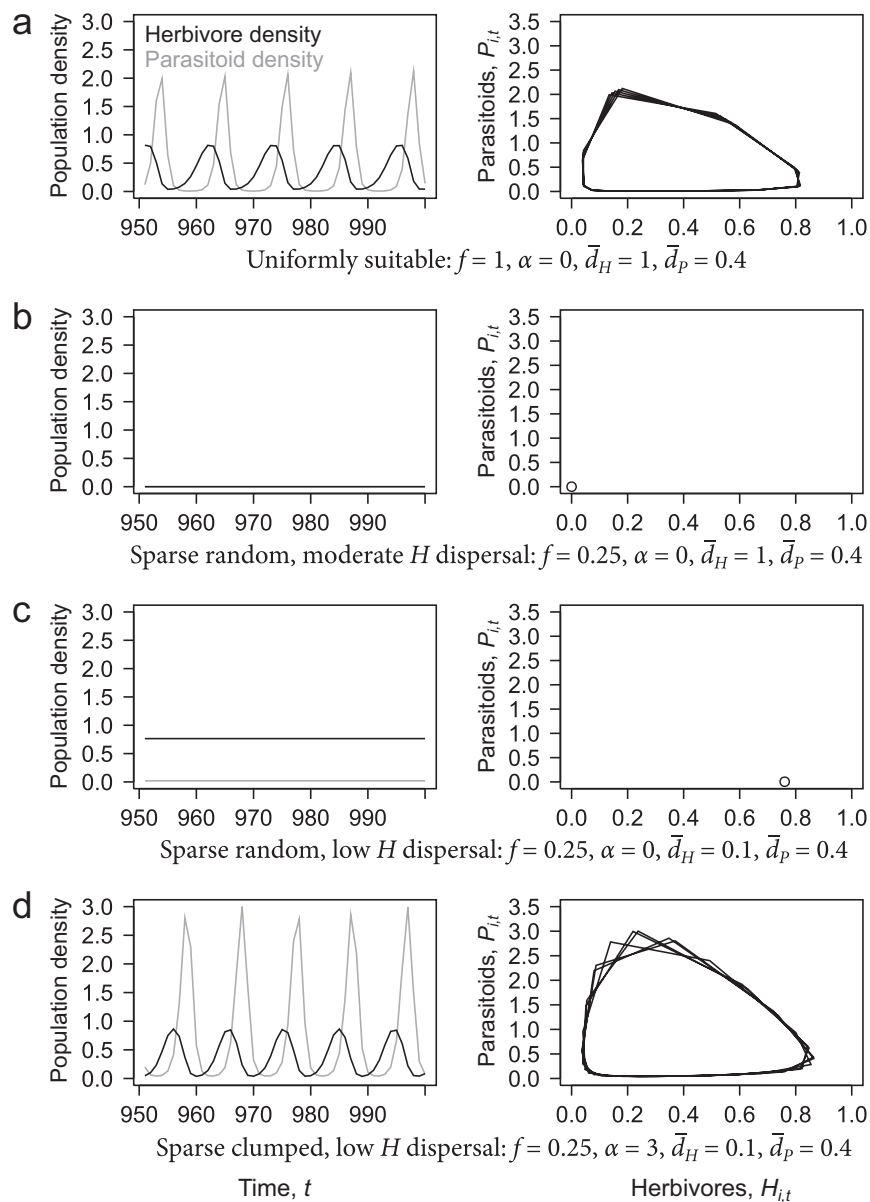
Figure 2: Examples of the effect of habitat removal on model behavior (baseline parameter values are given in table 1). Time series are on the left, and phase portraits are on the right. In *a* all habitat is suitable. *b* shows that if 75% of habitat is removed and the remaining habitat is distributed randomly, then herbivore populations become extinct. *c* shows that if herbivores do not disperse very far ($\bar{d}_H = 0.1$), however, removing 75% of habitat causes parasitoid extinction and persistently high herbivore density. Removing 75% of habitat when habitat is clumped instead causes a smaller increase in herbivore density and allows high-amplitude cycles to persist, as shown in *d*. *d* is more similar to *a* than to *c*, thus showing that clumping of habitat can mitigate the effect of habitat loss. Meanwhile, the larger-amplitude cycles in *d* versus *a* likely occur because higher dispersal mortality slows the response of parasitoids to increasing herbivore density. Each panel shows dynamics from a representative location, such that the average herbivore density over time at the location is approximately equal to the average herbivore density over the whole landscape ($1/200 \times \sum_{t=801}^{1,000} H_{i,t} \approx \bar{H}$).

($\bar{d}_P = 0.4$ km) and high ($\bar{d}_P = 1$ km) parasitoid dispersal distances (fig. 2*a* vs. 2*c*, panels I and II of fig. 3*a*). Herbivores can also benefit from habitat loss when dynamics are stable, but only if herbivore densities are low and parasitoid densities are high (fig. 3*b* vs. 3*c*). In the stable case with abundant parasitoids, herbivores can benefit from habitat loss when parasitoid dispersal is not too low ($\bar{d}_P > 0.1$ km) and when *f* is not too small regardless of whether herbivore dispersal is low (all panels of fig. 3*b* except VI and IX). Appendix B shows that these generalities hold for a wide range
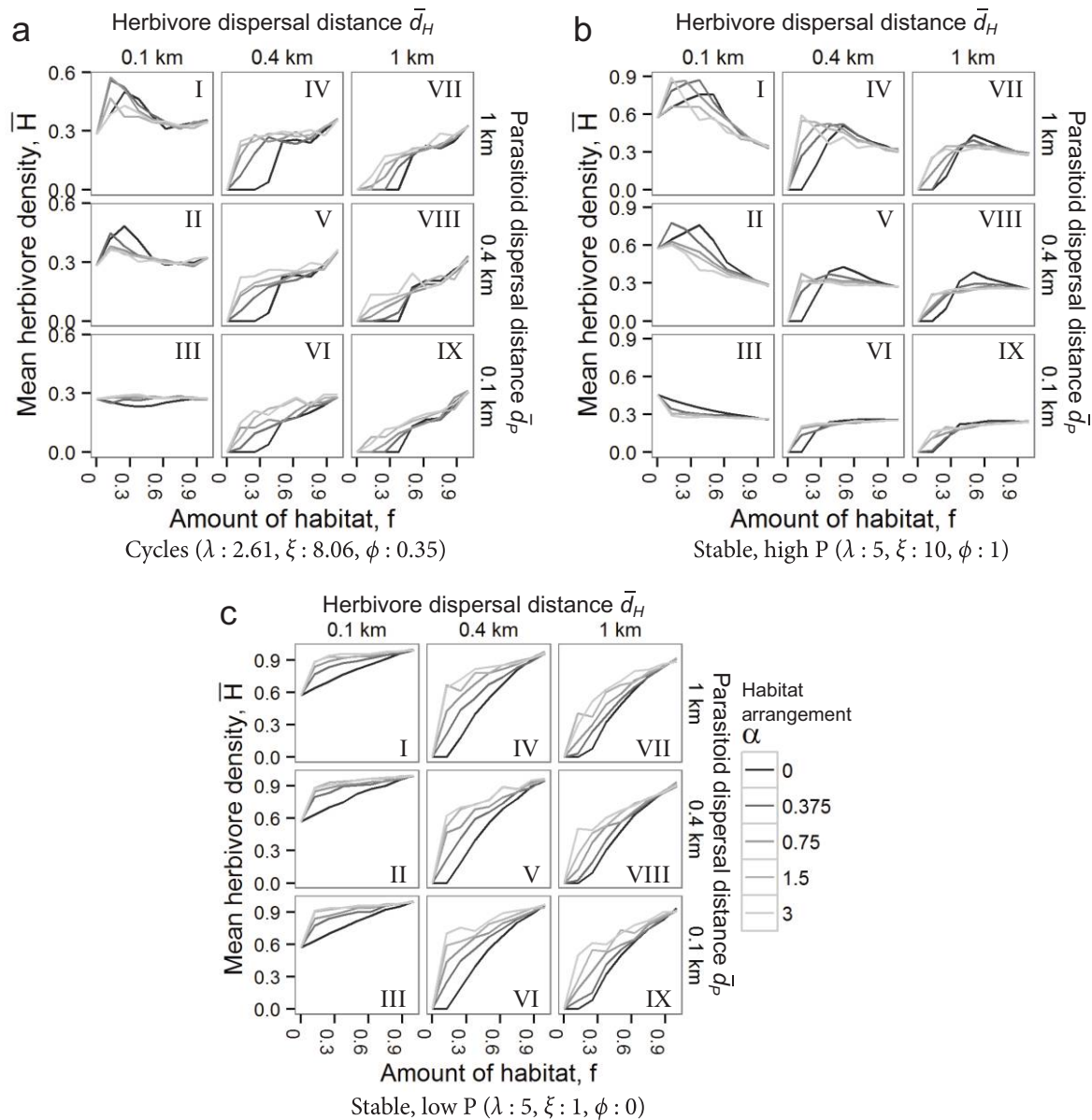
Figure 3: Effect of landscape configuration on mean herbivore density ($\overline{H}$) in three example cases of the forest tent caterpillar (FTC) model. Increasing lines indicate that mean herbivore density decreases with habitat removal, and decreasing lines indicate that mean herbivore density increases with habitat removal. Higher values of the habitat arrangement parameter α (lighter lines) produce landscapes in which suitable habitat is more clumped. *a* represents model behavior when dynamics are cyclic, which happens for estimated FTC parameter values (table 1); *b* and *c* are cases in which the dynamics are stable. In *b* herbivore density is low and parasitoid density is high, while in *c* herbivore density is high and parasitoid density is low.

of values of model parameters, although the magnitude of increase and the amount of habitat that leads to maximum herbivore density depend on habitat arrangement and other model parameters.

When dynamics are cyclic and habitat destruction leads to increased herbivore density, increased habitat clumping reduces the strength of the effect, so that the increase

in herbivore density with increasing habitat destruction is smaller (fig. 2*d* vs. 2*c*, panels I and II of fig. 3*a*). The effects of habitat loss and arrangement are generally smaller when dynamics are cyclic (fig. 3*a* vs. 3*b* and 3*c*) because in such cases the parasitoids keep the herbivore density well below carrying capacity even when habitat is abundant. Lines in figure 3 tend to have flatter slopes and more similarity to

one another when habitat is abundant (e.g., $f > 0.5$), indicating that the effects of habitat loss and arrangement are stronger when habitat is scarce. The effects of habitat loss and arrangement also depend on the dispersal distances ($\bar{d}_H$ and $\bar{d}_P$; fig. 3, app. B).

In this model, critical patch size—meaning the patch size below which either herbivores or parasitoids become extinct—depends on the demographic parameters and the dispersal distances of both parasitoids and herbivores (app. A). In many cases, our minimum patch size of 1 ha is smaller than the critical patch size for parasitoids (fig. 2*b*, 2*c*, all panels of fig. 3 except III) and for herbivores (fig. 2*b*, panels IV–IX of fig. 3). Nevertheless, hosts and parasitoids can persist because we consider landscapes that contain many hectares of suitable habitat. In other words, the persistence of parasitoids and herbivores depends on the amount and arrangement of habitat rather than the minimum patch size (as in fig. 2).

The Local Dispersal Success Approximation

Here we investigate whether the complex behavior of our spatial model can be understood using simpler nonspatial approximations. Dispersal success approximations account for interactions between habitat arrangement and the scale of dispersal without explicitly including space. So-called average dispersal success approximations attempt to predict whether populations persist on fragmented landscapes as a function of average dispersal success (VanKirk and Lewis 1997; Cobbold et al. 2005; Fagan and Lutscher 2006; Lutscher 2010). We propose a variant that we call the local dispersal-success approximation, which predicts population dynamics at each location as a function of dispersal success from that location. Local dispersal success is thus defined to be the proportion of animals dispersing from a given location that are expected to land in suitable habitat. Because we hypothesized that the effects of landscape configuration in our spatial model (figs. 2, 3) were caused by differences in dispersal mortality between trophic levels, we expected that a local dispersal success approximation could predict the effects of habitat arrangement in realistically complex landscapes with reasonable accuracy.

A local dispersal success approximation is most likely to be accurate if conditions are such that population growth can be ignored during the dispersal period, as in equation (1); if animal densities are similar in habitat patches that are near each other; and if the probability of dispersing from a location i to a nearby location j is equal to the probability of dispersing from j to i, as in equation (3). To show this, we first define herbivore dispersal success $S_{H,i}$ at location i on a discrete lattice as the probability that an animal from that location survives dispersal by landing in suitable habitat (VanKirk and Lewis 1997):

$$\underbrace{S_{H,i}}_{\text{dispersal success}} = \sum_{j=1}^{\Omega} \underbrace{k(d_{i,j}, \bar{d}_H)}_{\text{dispersal kernel}} I_j, \tag{5}$$

where I_j indicates whether habitat is suitable ($I_j = 1$) or unsuitable ($I_j = 0$) at location j. The dispersal kernel is again $k(.,.)$, and $\bar{d}_H$ is the average herbivore dispersal distance.

If locations i and j are near each other, there will be substantial dispersal between them. We construct a local dispersal success approximation by assuming that patches near location i have the same density of herbivores before dispersal, so that $\mathcal{H}_{i,t} = \mathcal{H}_{j,t}$ where $k(d_{i,j}, \bar{d}_H) \gg 0$. It follows that the population density of herbivores after dispersal allocation is proportional to the dispersal success from location i:

$$\underbrace{\mathcal{H}_{i,t}^* = \sum_j^{\Omega} k(d_{i,j}, \bar{d}_H)\mathcal{H}_{j,t}}_{\text{density after dispersal}} = \mathcal{H}_{i,t} \underbrace{\sum_j^{\Omega} k(d_{i,j}, \bar{d}_H)I_j}_{\text{dispersal success}} = \mathcal{H}_{i,t} S_{H,i}, \tag{6}$$

where $\mathcal{H}_{i,t}$ is the approximate population density of herbivores before dispersal. By an analogous argument, the population density of parasitoids after dispersal is proportional to the parasitoid's dispersal success: $\mathcal{P}_{i,t}^* = \mathcal{P}_{i,t} S_{P,i}$.

Substituting $\mathcal{H}_{i,t} S_{H,i}$ and $\mathcal{P}_{i,t} S_{P,i}$ from equation (6) into the full model, equation (1), then gives a local dispersal success approximation for population dynamics at each location i:

$$\mathcal{H}_{i,t+1} = h(S_{H,i}\mathcal{H}_{i,t}, S_{P,i}\mathcal{P}_{i,t}),$$
$$\mathcal{P}_{i,t+1} = g(S_{H,i}\mathcal{H}_{i,t}, S_{P,i}\mathcal{P}_{i,t}). \tag{7}$$

If equation (6) holds, the local dispersal success approximation, equation (7), is exactly equal to the spatial model, equation (1). The only requirement for the approximation to work well is thus that organism density is similar in habitat patches that are near one another.

The requirement of equation (6) is less restrictive than it might at first appear. Because dispersal is local, so that $k(d_{i,j}, \bar{d}_x) = 0$ when i is far from j, equation (6) can hold even if animal density varies substantially among distant locations. Moreover, forest insect population dynamics are typically spatially synchronized over at least moderate distances (Peltonen et al. 2002; Liebhold et al. 2004), meaning that insect densities in nearby locations rise and fall together. Accordingly, even though insect densities vary substantially over time, it may be reasonable to expect that, at any given time, densities of insects in nearby locations will be similar, in which case the approximation will be accurate.

To assess the utility of the local dispersal success approximation, we compare it to an average dispersal success approximation and to a mean field approximation. The average dispersal success approximation predicts global herbivore density as a function of a global measure of land-

scape configuration (VanKirk and Lewis 1997). Average dispersal success is defined as

$$S_x = \frac{\sum_{i=1}^{\Omega} S_{x,i}}{\sum_{i=1}^{\Omega} I_i}, \qquad (8)$$

where $S_{x,i}$ is the dispersal success of trophic level x at location i and I_i indicates whether location i provides suitable habitat. An average dispersal approximation is then obtained by setting $\mathcal{H}_{i,t}^* = S_H \mathcal{H}_{i,t}$ and $\mathcal{P}_{i,t}^* = S_P \mathcal{P}_{i,t}$ in equation (1). The average dispersal success approximation thus differs from the local dispersal success approximation in not accounting for differences in population dynamics among

locations. In the mean-field approximation, we further simplify by assuming that the only effect of dispersal is that a fraction of herbivores and parasitoids land in unsuitable habitat and die (Dieckmann et al. 2000), which is equivalent to setting $\mathcal{H}_{i,t}^* = f\mathcal{H}_{i,t}$ and $\mathcal{P}_{i,t}^* = f\mathcal{P}_{i,t}$ in equation (1).

To compare our approximation to the full model, we calculated the error ϵ as the difference in the herbivore density between the approximation and the full model, averaged over space and time. Because herbivore density is bounded by the carrying capacity, ϵ ranges from -1 to 1. Figure 4 shows that ϵ depends on both spatial and temporal variability in herbivore density, as measured by the standard deviation calculated over either time or space, as ap-
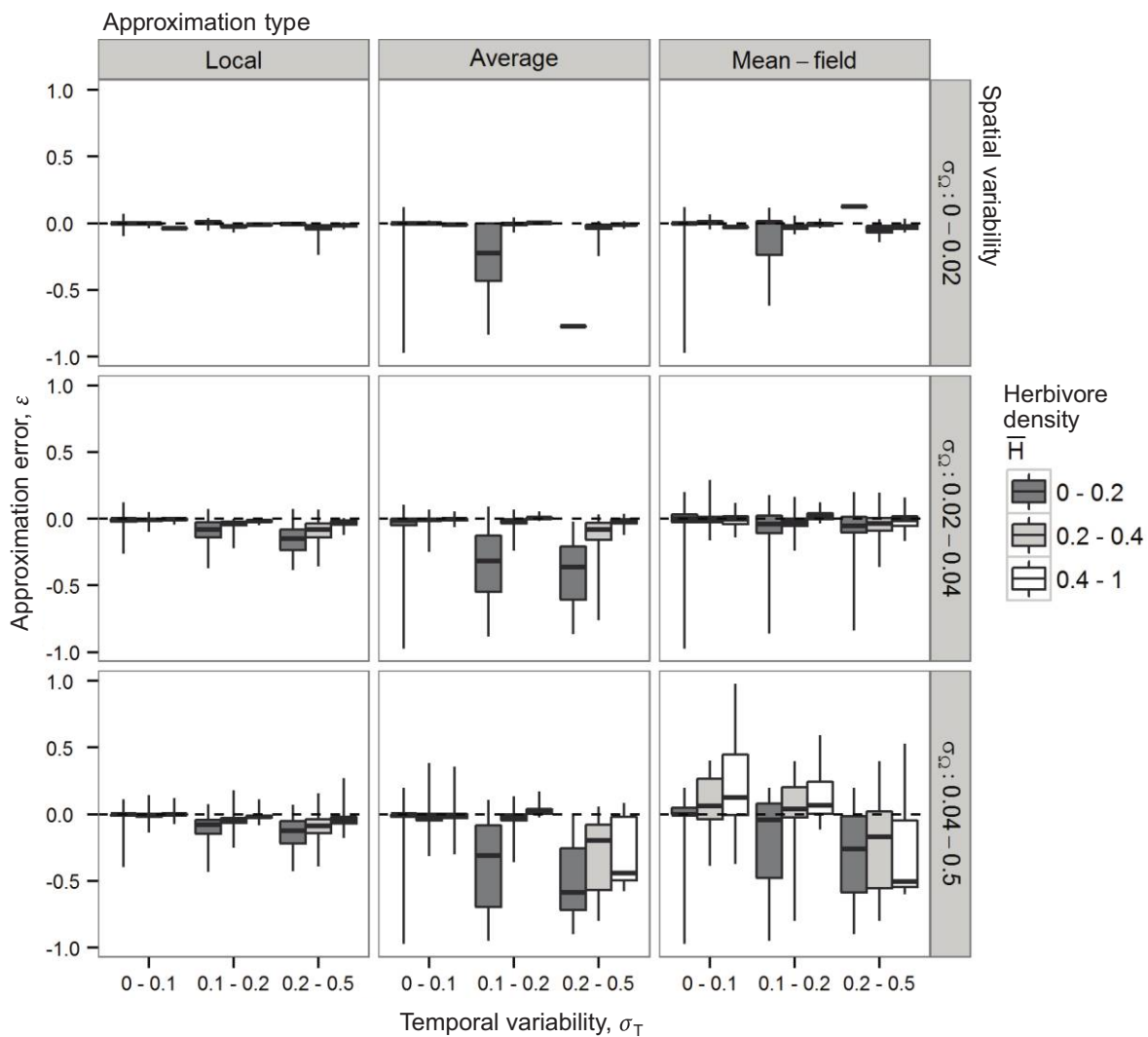

Figure 4: Effects of temporal variability (σ_T), spatial variability (σ_Ω), and mean herbivore density ($\overline{H}$) on the accuracy of three approximations. Zero values (dotted lines) indicate agreement between the full model and the approximation, negative errors indicate that the approximation substantially overpredicts mean herbivore density, and positive errors indicate substantial underprediction. The boxes extend from the 25th to the 75th percentile of errors, and the whiskers show the full range.

propriate. Crucially, however, the error in the local dispersal success approximation is considerably smaller than the error in the other two approximations. When spatial variability is low, the error in the local dispersal approximation is very small, independent of temporal variability, while the errors in the average dispersal success approximation and the mean field are slightly higher and dramatically more variable. Increasing the spatial variability leads to a mild increase in the error of the local dispersal success approximation, but it leads to a very substantial increase in the error in the other two approximations, especially if temporal variability is also high. A comparison of panels VII and III in figure 5 shows that the error in the local dispersal success approximation increases (larger negative numbers) as the amount of habitat increases and that the effect is most pronounced when parasitoid and herbivore dispersal are both low. This is because local peaks in abundance occur when population cycles are pronounced and dispersal is low, thereby violating the assumption that herbivore density is the same in nearby patches. The error similarly increases as the habitat parameter α increases, which leads to more clumped spatial distributions.

Irrespective of these trends, the error in the local dispersal success approximation is quite small. Given this low error, we conclude that the local dispersal success approximation can predict the behavior of the full spatial model with reasonable accuracy. This in turn suggests that the effects of landscape configuration are mostly due to variation in dispersal mortality among locations. That is, herbi-

vores benefit from habitat loss mostly because parasitoids suffer high dispersal mortality, not because of parasitoid-free refuges or some other mechanism.

An additional benefit of the local dispersal success approximation is that it greatly reduces computational costs. For example, our simulations of the full model required $\approx 3^{13}$ arithmetic operations, while the approximations required $\approx 7^8$ operations, a reduction of approximately 45,000-fold. The approximation also allows us to better understand model dynamics by simplifying the problem. First, for given values of the habitat fraction f, the habitat arrangement α, and the dispersal distances $\bar{d}_H$ and $\bar{d}_P$, we can calculate the distribution of dispersal success values across the landscape. The local dispersal success approximation can then be used to predict herbivore density from equation (7), which allows us to develop a qualitative understanding of how dispersal success determines herbivore density. Specifically, for each local dispersal success value we can predict herbivore density, as indicated by the shading in figure 6, while simultaneously summarizing the distribution of dispersal success values on the landscape using polygons that encompass the range of observed values of dispersal success (fig. 6; app. D). By examining the shading inside the polygons, we can see the range of herbivore densities expected in the given landscape type.

If habitat is abundant and dispersal success is high ($f = 1$, $\bar{d}_H = 1$, and $\bar{d}_H = 0.4$), then polygon A in figure 6a shows that the local dispersal success approximation accurately predicts the intermediate herbivore population
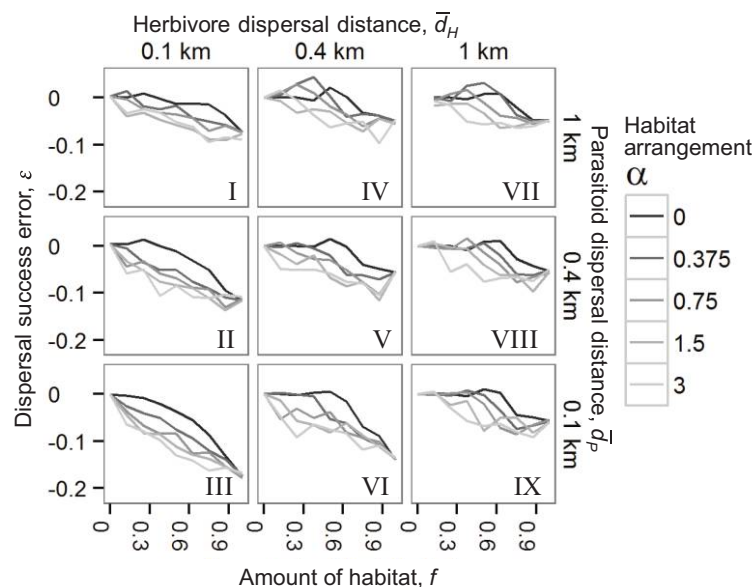

Figure 5: Effect of landscape configuration on the performance of the local dispersal success approximation (ϵ) in the forest tent caterpillar model given baseline parameter values (λ: 2.61, ξ: 8.06, φ: 0.35). Errors are larger when dispersal distances for both herbivores and parasitoids are low (panel III) or when habitat is clumped (light gray lines), both of which increase spatial variability.
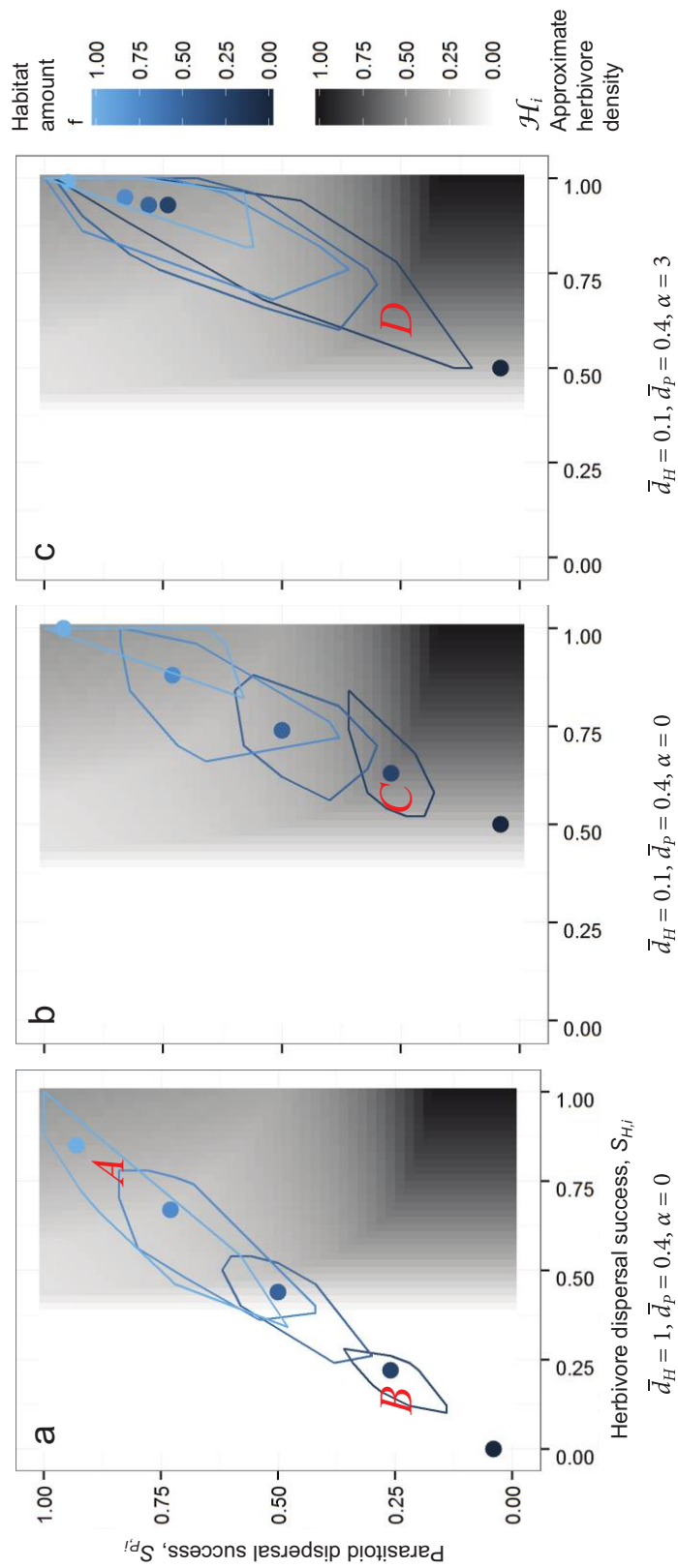
Figure 6: Local dispersal success approximation of mean herbivore density ($\mathcal{H}_i$) for the forest tent caterpillar model, using the baseline parameter values in table 1. The polygons are convex hulls that delineate variation in dispersal success on a landscape. The points indicate average dispersal success, and the shading indicates the herbivore density predicted (by eq. [7]) for each value of the herbivore and parasitoid local dispersal success. The four cases indicated by red letters (A–D) represent the four cases in figure 2. On landscapes containing a single suitable habitat patch, there is no variation among locations, so the local dispersal success approximation is equal to the average dispersal success approximation (dark blue points without polygons).

densities seen in figure 2a. Given these higher dispersal values, removing 75% of habitat substantially reduces the herbivore dispersal success, and so polygon B in figure 6a shows that the local dispersal success approximation accurately predicts the herbivore population collapse seen in figure 2b. For our lowest value of herbivore dispersal ($\bar{d}_H = 0.1$), removing 75% of habitat causes more moderate reductions in herbivore dispersal success, and so polygon C in figure 6b shows that the local dispersal success approximation accurately predicts the high average herbivore densities seen in figure 2c. Meanwhile, clumping of habitat increases the dispersal success of both trophic levels and therefore can mitigate the effects of habitat loss, such that polygon D in figure 6c shows that the local dispersal success approximation accurately predicts the return to intermediate herbivore population densities seen in figure 2d.

The approximation thus shows that herbivores are most likely to benefit from habitat removal when small reductions in parasitoid dispersal success substantially benefit herbivores, and it allows easy identification of the parameter values that lead to this result (app. D). Given a new model, one could therefore use the local dispersal success approximation to quickly assess whether herbivores are likely to benefit from habitat removal without simulating any landscapes. The summary view provided by the approximation also shows why the local dispersal success approximation performs better than the average dispersal success approximation in some cases (fig. 4). Both approximations are accurate in cases for which spatial variability is low and for which there is no variation in predicted herbivore density across the range of local dispersal success values, as in the particular case of polygon B in figure 6a. However, in cases for which the range of local dispersal success predictions is large, as in polygon D in figure 6c, the local dispersal success approximation is much more accurate.

Comparison to Data

Fragmentation of aspen forests in Ontario and Alberta has led to longer FTC outbreaks (Roland 1993, 2005; Roland and Taylor 1997; Cooke and Roland 2000) and lower parasitism rates (Roland and Taylor 1997; Rothman and Roland 1998). Here, we ask whether our model can explain these empirical results. When comparing our model to the data, however, an important point is that Roland (1993) recorded outbreaks at the scale of townships, which are areas of 100 km². Roland then measured outbreak duration as the number of years that the defoliated area exceeded 30% of a township area over a 34-year period, such that a forest was considered defoliated if more than 26% of its foliage had been damaged (Candau and Fleming 2005). To match this statistic, we first converted herbivore population density to percent defoliation. Densities of 4 moths per trap are associated with approximately 30% defoliation, while densities of 13 moths per trap are associated with 80% defoliation (Roland 2005). Taking the latter number as an estimate of carrying capacity, we assume that a forest is defoliated when herbivore density exceeds 4/13, or roughly 30% of carrying capacity. Regional duration is then the proportion of years in which defoliated area exceeds 30% of landscape area.

Figure 7a shows it is at least possible for outbreak duration to increase with increasing forest edge. For most values of herbivore and parasitoid dispersal distance, regional outbreak duration decreases with increasing forest edge. If, however, the herbivore dispersal distance is low, the parasitoid dispersal distance is intermediate, and the edge fraction is not too high, then outbreak duration increases as the amount of forest edge increases (panel II of fig. 7a). The same effect occurs less strongly when both dispersal distances are intermediate (panel V of fig. 7a) and when herbivore dispersal distance is low and parasitoid dispersal distance is high (panel I of fig. 7a). We thus argue that our model suggests a new and interesting explanation for patterns described by Roland (1993).

Moreover, the pattern observed in the data is initially surprising, yet the model explanation is reasonably simple. Specifically, outbreak duration increases with increasing forest edge because when parasitoids disperse farther than herbivores, a lack of suitable habitat causes high mortality of parasitoids during dispersal. The beneficial effect of these parasitoid losses on herbivore populations outweighs the increased dispersal mortality of herbivores. Habitat destruction can therefore benefit herbivores more than it harms them. Our model thus provides a possible explanation for the effects of forest fragmentation on both outbreak duration and outbreak dynamics.

Our model can also aid in interpreting differences between studies. For example, Wood et al. (2010) observed that forest fragmentation instead decreased FTC outbreak duration in more southerly mixed forests of New York, Massachusetts, Vermont, and New Hampshire and concluded that the effects of fragmentation differ between northern and southern forests (Roland 1993, 2005; Roland and Taylor 1997; Cooke and Roland 2000). Wood et al. (2010), however, measured outbreak duration at point locations rather than over the 100-km² areas over which outbreaks were measured by Roland and colleagues. This is important because in our model the duration of regional-scale outbreaks in some cases can increase as forest edge density increases, but the duration of local-scale outbreaks can only decrease or remain the same as edge density increases (fig. 7b). More generally, local-scale and regional-scale durations in the model are not strongly correlated with each other (Spearman correlation coefficient of −0.08 over all simulations). Our model thus suggests that studies measuring
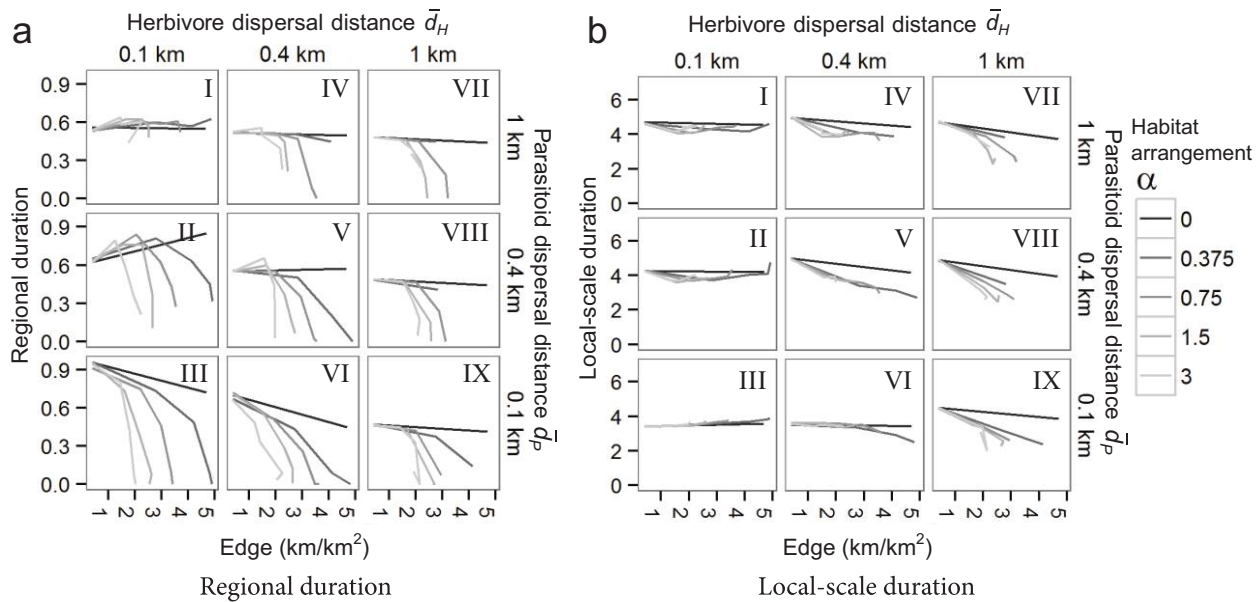
Figure 7: Effects of landscape configuration and dispersal on the duration of forest tent caterpillar outbreaks. Regional duration is the proportion of years in which defoliated area exceeds 30% of landscape area, and local-scale duration is the average outbreak duration at point locations. Lines are averages over five replicate landscapes for each combination of parameter values. Cooke and Roland (2000) and Roland (1993) did not observe landscapes containing <50% habitat or >3 km/km² of edge, so we excluded landscapes containing <50% habitat or >5 km/km² of edge. At the left end of each line, $f = 1$. Local-scale outbreak duration is undefined in noncyclic cases, so those cases have been omitted.

regional-scale (Roland 1993, 2005; Roland and Taylor 1997; Cooke and Roland 2000) and local-scale (Wood et al. 2010) duration are not comparable, and so the data are not sufficient to allow us to determine whether the effects of fragmentation differ among forest types.

Discussion

In nature, specialist predators are often observed to suffer more from habitat loss or fragmentation than prey or generalist predators, and release from predation can therefore cause host/prey density or occupancy to increase as habitat is removed from a landscape (Kruess and Tscharntke 1994; Cappuccino et al. 1998; Denys and Schmidt 1998; Gibb and Hochuli 2002; Tscharntke et al. 2002; Cronin and Reeve 2005; Holyoak et al. 2005; Ryall and Fahrig 2006; Cagnolo et al. 2009; Chase et al. 2010; Driscoll et al. 2010). Models aimed at explaining this pattern, however, generally ignore mortality from dispersal into unsuitable habitat and predict that habitat loss will benefit prey when prey are more mobile than predators (Ryall and Fahrig 2006; Holt and Barfield 2009). Our model, in contrast, does include dispersal mortality, and it therefore makes the opposite prediction that habitat loss is most likely to benefit herbivores when herbivores are less mobile than parasitoids (fig. 3, app. B). A spatial model of larch budmoth

(*Zeiraphera diniana* Guenee) gives similar results (Hughes 2012). Dispersal mortality has not been previously identified as a possible explanation for increasing herbivore or prey density with increasing habitat loss.

Our model also suggests that high parasitoid dispersal mortality can explain why increased patchiness leads to longer FTC outbreaks (fig. 7). Roland and colleagues argued that the increase in outbreak duration with increasing fragmentation may be due to the effects of fragmentation on parasitoid behavior (Roland 1993, 2005; Roland and Taylor 1997; Cooke and Roland 2000) but were later concerned by the lack of evidence in support of this hypothesis (Roth et al. 2006). Our work shows that the effect of forest fragmentation on outbreak duration could simply be an effect of increased mortality on dispersing parasitoids. Parasitoid dispersal rates in nature are indeed often high (Hastings 2000; McCann et al. 2000; Elzinga et al. 2007; Henne et al. 2007). A mark-recapture experiment indicates that FTC parasitoids can travel at least 300 m, but a low recapture rate (3/3,000) precludes accurate estimation of average or maximum dispersal distance of parasitoids (Roland and Taylor 1995; Cobbold et al. 2005). Virtually nothing is known about parasitoid dispersal mortality, so further testing of our model predictions would require additional data.

Our model further suggests a possible explanation for the results of Roth et al. (2006), who found no evidence

that the density of the specialist FTC parasitoid *Arachnidomyia aldrichi* was lower in forest fragments, contrary to other studies (Roland and Taylor 1997; Rothman and Roland 1998). Roth et al. (2006), however, studied areas with low FTC densities, and in such cases our model predicts that specialist parasitoid density should be very low. We thus would not expect to see large effects of fragmentation on parasitism in these conditions, and Roth et al. (2006) may therefore simply not have had sufficient statistical power to detect the small effects of fragmentation that actually may have been present.

Fragmentation may also affect processes other than dispersal mortality (Andrén 1994; Rothman and Roland 1998; Ewers and Didham 2006; Roth et al. 2006). Many parasitoids rely on chemical cues to locate their hosts (Vet and Dicke 1992; Godfray 1994; Mondor and Roland 1997, 1998), and wind patterns in open areas can disrupt chemical signals (Amman and Logan 1998), so fragmentation could instead alter parasitoid search efficiency. Solar exposure, which increases with increasing fragmentation, can benefit FTCs by inactivating nuclear polyhedrosis virus (Rothman and Roland 1998). Existing evidence is not sufficient to distinguish among these possibilities, but additional insight might be gained by comparing the ability of alternative models to predict observed patterns.

We used a simple dispersal model because we did not have sufficient information to justify or to estimate the parameters of more complex dispersal models (Baltensweiler and Rubli 1999; Cobbold et al. 2005). In reality, forest insects sometimes mitigate dispersal risks by using chemical or visual cues (Greenbank et al. 1980; Schneider 1992; Vet and Dicke 1992; Godfray 1994; Baltensweiler and Rubli 1999; Pureswaran et al. 2000; Cronin and Reeve 2005; Ryall and Fahrig 2006; Cronin 2009) or by using density-dependent dispersal strategies (Bowler and Benton 2005; Geritz et al. 2009; Green 2009; Travis et al. 2009). Our simple model nevertheless provides a useful starting point.

The local dispersal success approximation does not account for the redistribution of animals from areas of high density to areas of lower density, yet it still accurately predicts the behavior of the full spatial model. We therefore conclude that dispersal mortality plays a crucial role in our model, while the redistribution of animals has a much smaller effect on average herbivore density. The local dispersal success approximation could also be used to estimate dispersal parameters from widely available data. Although herbivore dispersal parameters can sometimes be estimated from the relationship between pupal density or herbivore damage and adult moth density (Anderson and Sturtevant 2011), in general estimating densities across large landscapes is logistically impractical. The local dispersal success approximation (eq. [6]) suggests that it may be possible to estimate herbivore dispersal distance $\bar{d}_H$ from a combination of data on the distribution of habitat across landscapes (I_j in eq. [6]), which are widely available, and from pre- and postdispersal population density estimates at a few sample locations ($\mathcal{H}_{i,t}$ and $\mathcal{H}_{i,t}^*$ in eq. [6]).

Local dispersal success is a patch-based measure of connectivity that arises naturally from integrodifference models, making underlying assumptions about movement clear and explicit (Kadoya 2009). The approximation is closely related to the incidence function measure (Moilanen and Hanski 1998; Schooley and Branch 2007; Kadoya 2009), which has been criticized for assuming that dispersal is random (Kadoya 2009). We therefore emphasize that the dispersal success approximation requires only reciprocal dispersal, so that the probability of dispersing from a location i to a nearby location j is equal to the probability of dispersing from j to i. The dispersal success approximation is thus useful even if the dispersal rate depends on population density or if animals preferentially disperse to suitable habitat patches.

Although local dispersal success is an imperfect measure of functional landscape connectivity, it may be preferable to other common methods of assessing the relationship between landscapes and animals. For example, a common approach is to examine correlations among landscape measures and population features at multiple spatial scales, using these correlations to identify the scale of interaction between animals and their habitats (Roland 1993; Roland and Taylor 1997; Cooke and Roland 2000; Boccaccio and Petacchi 2009; Driscoll et al. 2010; Wood et al. 2010). Such an approach assumes that, within a neighborhood, all locations are weighted equally, which is equivalent to assuming a truncated uniform dispersal kernel. For most organisms, however, a more reasonable assumption is that dispersal probability declines with distance, and kernel-weighted connectivity measures such as local dispersal success are therefore likely to be more useful.

Acknowledgments

APPENDIX A

Linear Stability Analysis of the Nonspatial FTC Models: Conditions for Host and Parasitoid Viability

Local dispersal success approximations of the spatial model (eqq. [1], [2]) are obtained by setting $H_{i,t}^* = S_{H,i}H_{i,t}$ and $P_{i,t}^* = S_{P,i}P_{i,t}$ (eq. [7]). A nonspatial model (with no dispersal) is a special case of a local dispersal success approximation in which herbivore and parasitoid dispersal success is 100% ($S_{H,i} = S_{P,i} = 1$). An average dispersal approximation is obtained by setting $H_{i,t}^* = S_H H_{i,t}$ and $P_{i,t}^* = S_P P_{i,t}$, and a mean-field approximation is obtained by setting $H_{i,t}^* = fH_{i,t}$ and $P_{i,t}^* = fP_{i,t}$. Thus, on a suitable habitat patch ($I_i = 1$), the nonspatial model and all approximations are special cases of the following model:

$$H_{i,t+1} = \lambda S_{H,i} H_{i,t} e^{-\log(\lambda)S_{H,i}H_{i,t}} e^{-S_{P,i}P_{i,t}},$$
$$P_{i,t+1} = \xi S_{H,i} H_{i,t} \left(1 - e^{-S_{P,i}P_{i,t}}\right) e^{-\varphi\log(\lambda)S_{H,i}H_{i,t}}. \tag{A1}$$

The conditions for herbivore and parasitoid viability for the nonspatial model and all approximations can thus be obtained by analyzing the stability of equation (A1). Note that Cobbold et al. (2009) analyzed the nonspatial FTC model; here, we present the more general case (eq. [A1]). Without parasitoids, the herbivore equilibrium for equation (A1) is

$$\hat{H}_i = \frac{\log(\lambda S_{H,i})}{\log(\lambda)S_{H,i}}. \tag{A2}$$

In a system without parasitoids, the herbivore equilibrium is stable when $0 < \log(\lambda S_{H,i}) < 2$. When herbivore growth rate is too low ($\log(\lambda S_{H,i}) < 0$), herbivores are not viable, and high herbivore growth rates ($\log(\lambda S_{H,i}) \gg 2$) cause chaotic fluctuations.

Parasitoids can invade when the herbivore-only equilibrium is stable to perturbations in herbivore density (i.e., $0 < \log(\lambda S_{H,i}) < 2$) and unstable to perturbations in parasitoid density, so that the equilibrium $\hat{H}_i \neq 0$, $\hat{P}_i = 0$ is invasible by parasitoids. The eigenvalues of the Jacobian matrix of equation (A1) evaluated at the herbivore-alone equilibrium ($\hat{H}_i, \hat{P}_i = 0$) are

$$\mu_1 = 1 - \log(\lambda S_{H,i}),$$
$$\mu_2 = \frac{S_{P,i}\xi(S_{H,i}\lambda)^{-\varphi}\log(S_{H,i}\lambda)}{\log(\lambda)}. \tag{A3}$$

If herbivores are viable and stable ($0 < \log(\lambda S_{H,i}) < 2$), the absolute value of the first eigenvalue is always less than 1 ($|\mu_1| < 1$). Given the obvious constraints that $S_{H,i}$, $S_{P,i}$, Ω, and φ are between 0 and 1 and that growth rates λ and ξ are positive, the second eigenvalue is always positive ($\mu_2 \geq 0$). Thus, parasitoids are viable if the second eigenvalue is greater than 1. Special cases of this condition for parasitoid invasibility are given in table A1. Note that invasibility is a necessary but not sufficient condition for parasitoid persistence. The coexistence steady state can undergo a subcritical flip bifurcation (Neubert and Kot 1992), causing large amplitude cycles that drive parasitoids extinct.

The coexistence equilibrium for the general model (eq. [A1]) is

$$\hat{H}_i = \frac{\log(\lambda) + \log(S_{H,i}) - S_{P,i}P_i}{S_{H,i}\log(\lambda)},$$
$$\hat{P}_i = \frac{\xi(\log(\lambda S_{H,i}) - S_{P,i}P_i)}{\log(\lambda)} e^{-\varphi\log(\lambda S_{H,i})} \left(e^{\varphi z} - e^{S_{P,i}P_i(\varphi-1)}\right). \tag{A4}$$

Herbivores are viable if $\log(\lambda S_{H,i}) > 0$, so the critical patch size for herbivores depends on herbivore dispersal and λ. If herbivore density reaches 0 when the amount of habitat is small (app. B), we can conclude that the minimum patch size in the model is less than the critical patch size for herbivores. The condition for parasitoid invasibility in the local-dispersal success approximation (table A1) implies that the critical patch size for parasitoids depends on all demographic parameters and the dispersal distances of both parasitoids and herbivores. In most cases, our minimum patch size of 1 ha is smaller than the critical patch size for parasitoids, and our maximum patch size of 10,000 ha is larger than the critical patch size. Thus, parasitoids (and often herbivores) eventually become extinct as habitat is removed from the landscape.

Table A1: Conditions for parasitoid invasibility in the nonspatial forest tent caterpillar model and approximations

Approximation	Condition
Local dispersal success	$\frac{S_{P,i}\xi(S_{H,i}\lambda)^{-\varphi}\log(S_{H,i}\lambda)}{\log(\lambda)} > 1$
Average dispersal success	$\frac{S_P\xi(S_H\lambda)^{-\varphi}\log(S_H\lambda)}{\log(\lambda)} > 1$
Mean field	$\frac{f\xi(f\lambda)^{-\varphi}\log(f\lambda)}{\log(\lambda)} > 1$
Nonspatial	$\lambda^{-\varphi}\xi > 1$

APPENDIX B

Effects of Landscape Configuration on Herbivore Density

Figures B1–B4 show how the effects of changing the amount and arrangement of habitat depend on forest tent caterpillar demographic parameters.
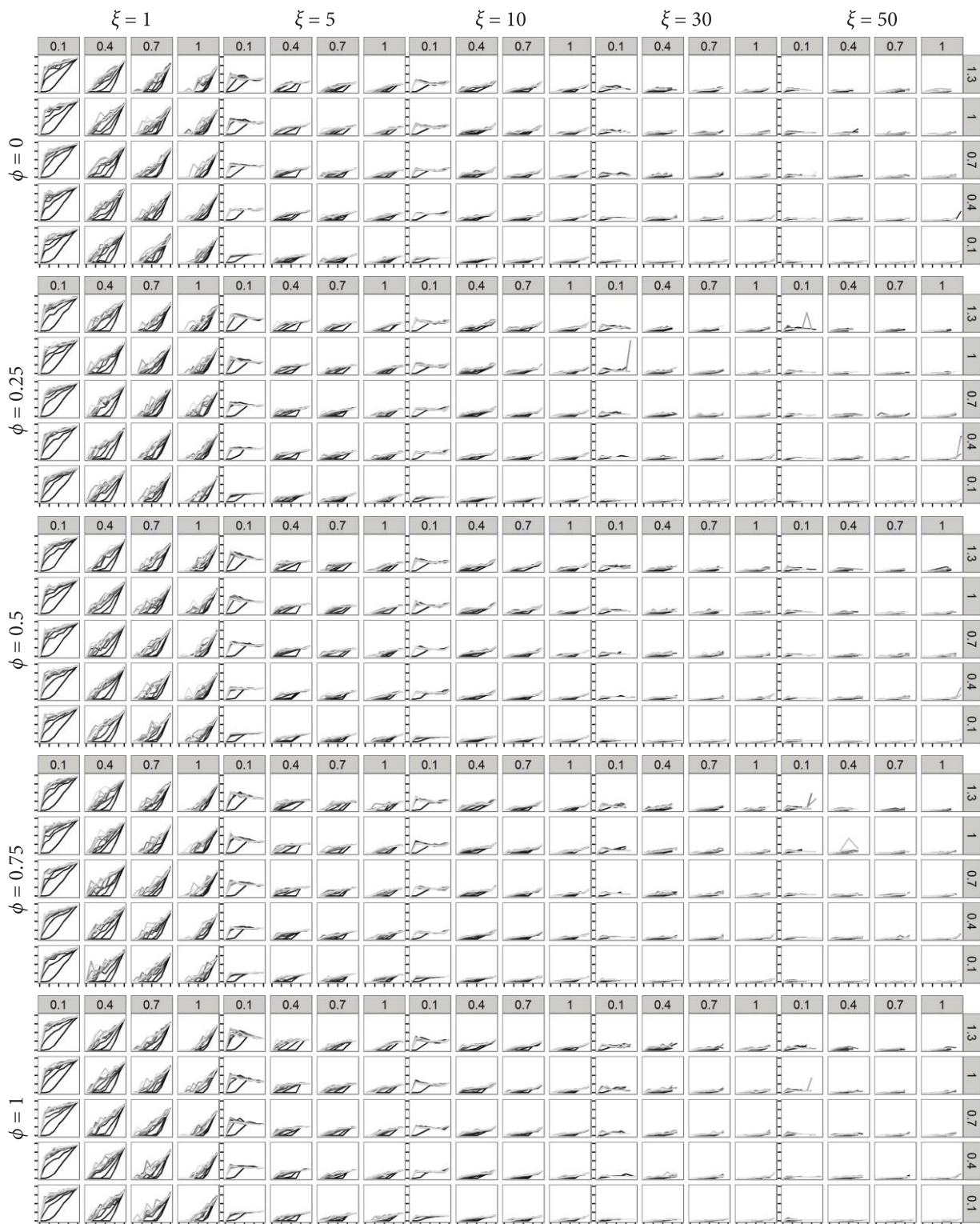
Figure B1: Average herbivore abundance ($\overline{H}$) in the forest tent caterpillar model (eq. [2]). Axis scales and legend are as in figure 3. Herbivore growth rate $\lambda = 1.5$. Parasitoid phenology φ and parasitoid dispersal $\bar{d}_P$ vary among rows. Parasitoid growth rate ξ and herbivore dispersal $\bar{d}_H$ vary among columns. Habitat abundance f varies along the X-axis, and color varies with habitat arrangement (α). Cases where parasitoids can invade according to the local dispersal success approximation but are extinct due to instability have been omitted.
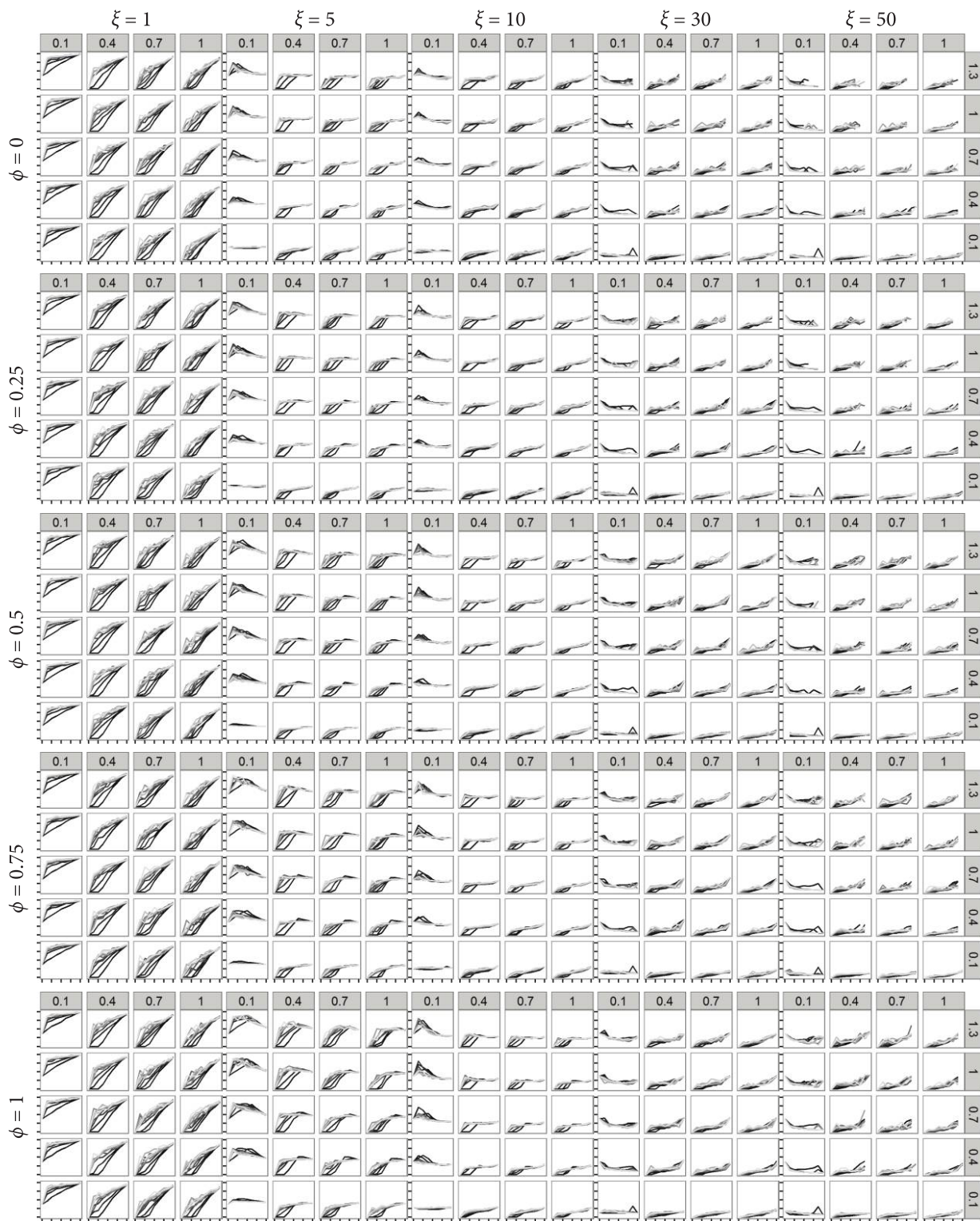
Figure B2: Average herbivore abundance ($\overline{H}$) in the forest tent caterpillar model. Herbivore growth rate $\lambda = 3$. See figure B1 for more details.

E000

Figure B3: Average herbivore abundance ($\overline{H}$) in the forest tent caterpillar model. Herbivore growth rate $\lambda = 5$. See figure B1 for more details.

E000

Figure B4: Average herbivore abundance ($\overline{H}$) in the forest tent caterpillar model. Herbivore growth rate $\lambda = 7$. See figure B1 for more details.
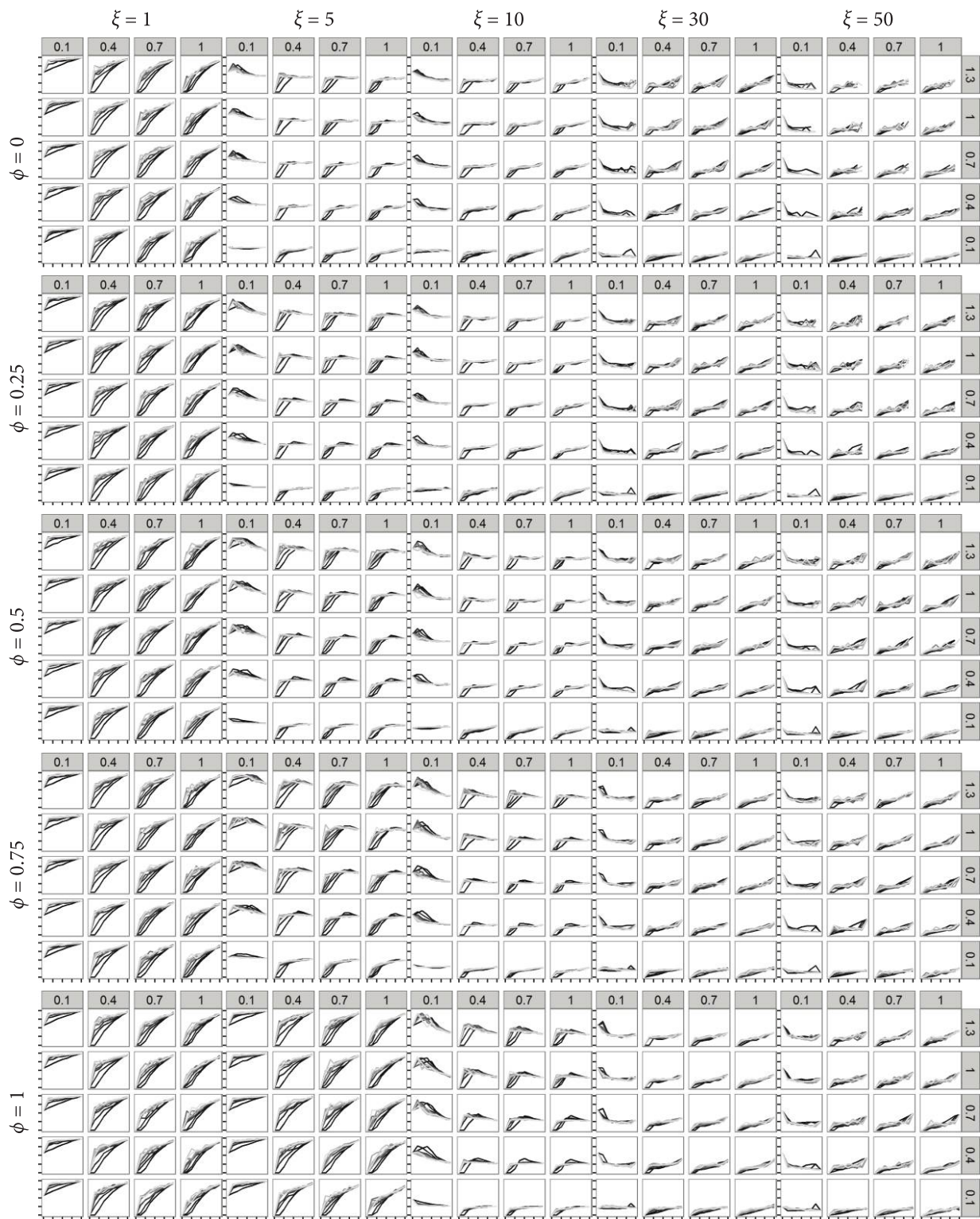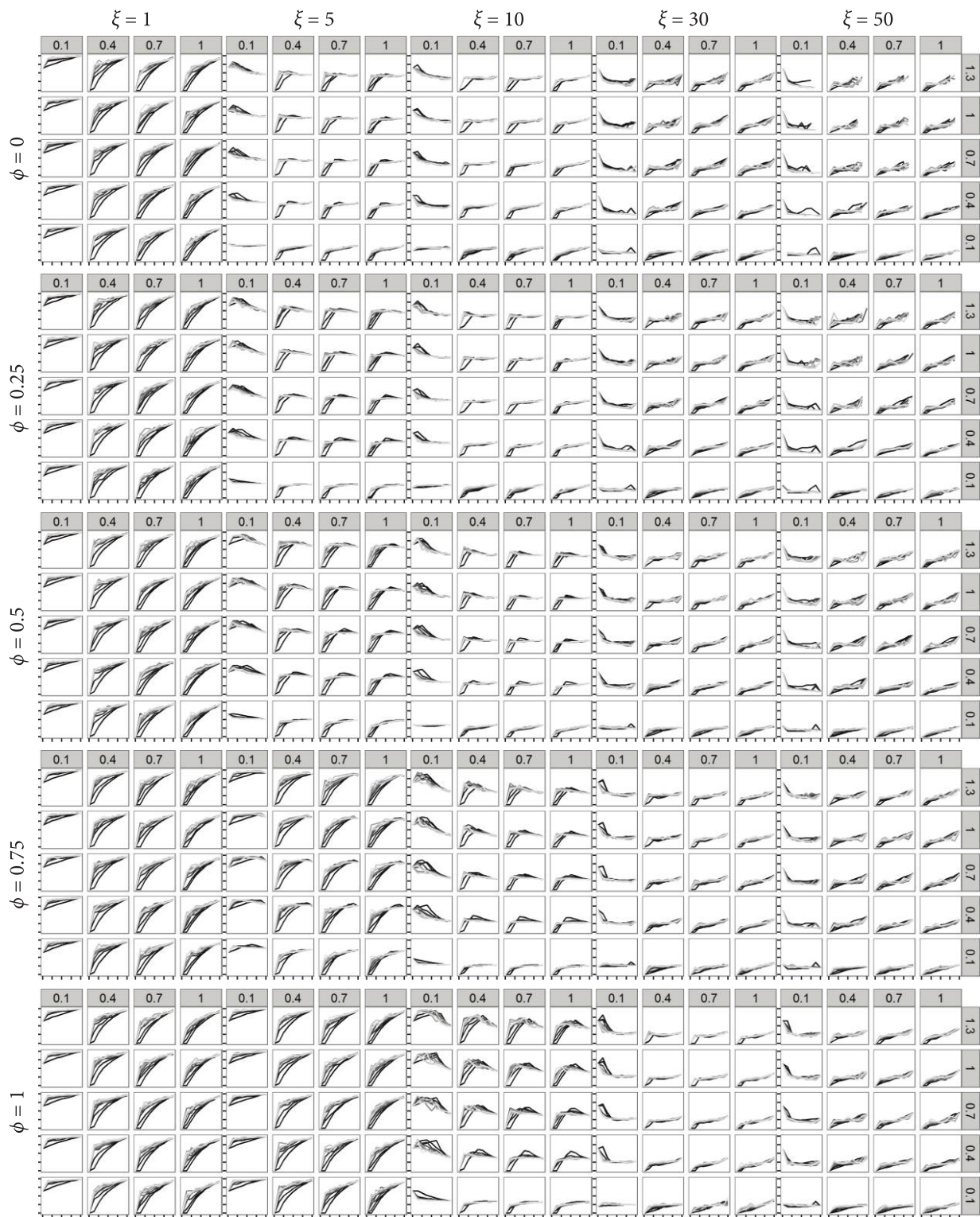
Literature Cited

Abbott, K. C., and G. Dwyer. 2008. Using mechanistic models to understand synchrony in forest insect populations: the North American gypsy moth as a case study. American Naturalist 172:613–624.

Abrams, P. A. 2002. Will small population sizes warn us of impending extinctions? American Naturalist 160:293–305.

———. 2009. When does greater mortality increase population size? the long history and diverse mechanisms underlying the hydra effect. Ecology Letters 12:462–474.

Amman, G. D., and J. A. Logan. 1998. Silvicultural control of mountain pine beetle: prescriptions and the influence of microclimate. American Entomologist 44:166–177.

Anderson, D. P., and B. R. Sturtevant. 2011. Pattern analysis of eastern spruce budworm *Choristoneura fumiferana* dispersal. Ecography 34:488–497.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat—a review. Oikos 71:355–366.

Babin-Fenske, J., and M. Anand. 2011. Agent-based simulation of effects of stress on forest tent caterpillar (*Malacosoma disstria* Hubner) population dynamics. Ecological Modelling 222:2561–2569.

Baltensweiler, W., and D. Rubli. 1999. Dispersal: an important driving force of the cyclic population dynamics of the larch bud moth, *Zeiraphera diniana* Gn. Forest Snow and Landscape Research 74:3–153.

Beddington, J., C. Free, and J. Lawton. 1976. Dynamic complexity in predator-prey model framed in simple difference equations. Nature 225:58–60.

Boccaccio, L., and R. Petacchi. 2009. Landscape effects on the complex of *Bactrocera oleae* parasitoids and implications for conservation biological control. Biocontrol 54:607–616.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205–225.

Cagnolo, L., G. Valladares, A. Salvo, M. Cabido, and M. Zak. 2009. Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. Conservation Biology 23:1167–1175.

Candau, J. N., and R. A. Fleming. 2005. Landscape-scale spatial distribution of spruce budworm defoliation in relation to bioclimatic conditions. Canadian Journal of Forest Research 35:2218–2232.

Cappuccino, N., D. Lavertu, Y. Bergeron, and J. Régnière. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. Oecologia (Berlin) 114:236–242.

Chase, J. M., A. A. Bergett, and E. G. Biro. 2010. Habitat isolation moderates the strength of top-down control in experimental pond food webs. Ecology 91:637–643.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80:1475–1494.

Cobbold, C. A., M. A. Lewis, F. Lutscher, and J. Roland. 2005. How parasitism affects critical patch-size in a host-parasitoid model: application to the forest tent caterpillar. Theoretical Population Biology 67:109–125.

Cobbold, C. A., J. Roland, and M. A. Lewis. 2009. The impact of parasitoid emergence time on host-parasitoid population dynamics. Theoretical Population Biology 75:201–215.

Cooke, B. J., and J. Roland. 2000. Spatial analysis of large-scale patterns of forest tent caterpillar outbreaks. Ecoscience 7:410–422.

Cronin, J. T. 2009. Habitat edges, within-patch dispersion of hosts, and parasitoid oviposition behavior. Ecology 90:196–207.

Cronin, J. T., and J. D. Reeve. 2005. Host-parasitoid spatial ecology: a plea for a landscape-level synthesis. Proceedings of the Royal Society B: Biological Sciences 272:2225–2235.

De Berg, M. 2000. Computational geometry: algorithms and applications. Springer.

Denys, C., and H. Schmidt. 1998. Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. Oecologia (Berlin) 113:269–277.

Diggle, P. J., and P. J. Ribeiro. 2006. Model-based geostatistics. Springer Series in Statistics. Springer, New York.

Driscoll, D. A., J. B. Kirkpatrick, P. B. McQuillan, and K. J. Bonham. 2010. Classic metapopulations are rare among common beetle species from a naturally fragmented landscape. Journal of Animal Ecology 79:294–303.

Dwyer, G., J. Dushoff, and S. H. Yee. 2004. The combined effects of pathogens and predators on insect outbreaks. Nature 430:341–345.

Elzinga, J. A., S. van Nouhuys, D. J. van Leeuwen, and A. Biere. 2007. Distribution and colonisation ability of three parasitoids and their herbivorous host in a fragmented landscape. Basic and Applied Ecology 8:75–88.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81:117–142.

Fagan, W. F., and F. Lutscher. 2006. Average dispersal success: linking home range, dispersal, and metapopulation dynamics to reserve design. Ecological Applications 16:820–828.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics 34:487–515.

Fitzgerald, T. D. 1995. The tent caterpillars. Cornell University Press, Ithaca, NY.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics 35:557–581.

Fortin, M. J., B. Boots, F. Csillag, and T. K. Remmel. 2003. On the role of spatial stochastic models in understanding landscape indices in ecology. Oikos 102:203–212.

Frolking, S., M. W. Palace, D. B. Clark, J. Q. Chambers, H. H. Shugart, and G. C. Hurtt. 2009. Forest disturbance and recovery: a general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure. Journal of Geophysical Research 114:G00E02.

Galik, C. S., and R. B. Jackson. 2009. Risks to forest carbon offset projects in a changing climate. Forest Ecology and Management 257:2209–2216.

Geritz, S. A. H., M. Gyllenberg, and P. Ondracek. 2009. Evolution of density-dependent dispersal in a structured metapopulation. Mathematical Biosciences 219:142–148.

Gibb, H., and D. Hochuli. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological Conservation 106:91–100.

Godfray, H. C. J. 1994. Parasitoids: behavioral and evolutionary ecology. Monographs in Behavior and Ecology. Princeton University Press, Princeton, NJ.

Green, D. M. 2009. Coevolution of dispersal in a parasitoid-host system. Population Ecology 51:253–260.

Greenbank, D. O., G. W. Schaefer, and R. C. Rainey. 1980. Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal—

new understanding from canopy observations, radar, and aircraft. Memoirs of the Entomological Society of Canada 110:1–49.

Hastings, A. 2000. Parasitoid spread: lessons for and from invasion biology. Princeton University Press, Princeton, NJ.

Henne, D. C., S. J. Johnson, and J. T. Cronin. 2007. Population spread of the introduced red imported fire ant parasitoid, *Pseudacteon tricuspis* Borgmeler (Diptera: Phoridae), in Louisiana. Biological Control 42:97–104.

Hirzel, A. H., R. M. Nisbet, and W. W. Murdoch. 2007. Host-parasitoid spatial dynamics in heterogeneous landscapes. Oikos 116:2082–2096.

Holt, R. D., and M. Barfield. 2009. Trophic interactions and range limits: the diverse roles of predation. Proceedings of the Royal Society B: Biological Sciences 276:1435–1442.

Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago.

Hughes, J. 2012. Patterns and processes in forest insect population dynamics. PhD thesis. University of Toronto. Accessed March 16, 2015. http://hdl.handle.net/1807/34060.

James, P. M. A., D. W. Coltman, B. W. Murray, R. C. Hamelin, and F. A. H. Sperling. 2011. Spatial genetic structure of a symbiotic beetle-fungal system: toward multi-taxa integrated landscape genetics. PLoS ONE 6:e25359.

Jang, S. R. J., and D. M. Johnson. 2009. Dynamics of discrete-time larch budmoth population models. Journal of Biological Dynamics 3:209–223.

Johnson, D. M., A. M. Liebhold, P. C. Tobin, and O. N. Bjornstad. 2006. Allee effects and pulsed invasion by the gypsy moth. Nature 444:361–363.

Jones, E., T. Oliphant, P. Peterson, et al. 2001. SciPy: open source scientific tools for Python. http://www.scipy.org.

Kadoya, T. 2009. Assessing functional connectivity using empirical data. Population Ecology 51:5–15.

Keitt, T. H. 2000. Spectral representation of neutral landscapes. Landscape Ecology 15:479–493.

Kindlmann, P., and F. Burel. 2008. Connectivity measures: a review. Landscape Ecology 23:879–890.

Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. Science 264:1581–1584.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990.

Liebhold, A., W. D. Koenig, and O. N. Bjornstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology Evolution and Systematics 35:467–490.

Lutscher, F. 2010. Nonlocal dispersal and averaging in heterogeneous landscapes. Applicable Analysis 89:1091–1108.

Malmstrom, C. M., and K. F. Raffa. 2000. Biotic disturbance agents in the boreal forest: considerations for vegetation change models. Global Change Biology 6:35–48.

McCann, K., A. Hastings, S. Harrison, and W. Wilson. 2000. Population outbreaks in a discrete world. Theoretical Population Biology 57:97–108.

McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology and Evolution 26:523–532.

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79:2503–2515.

Mondor, E. B., and J. Roland. 1997. Host locating behaviour of *Leschenaultia exul* and *Patelloa pachypyga*: two tachinid parasitoids of the forest tent caterpillar, *Malacosoma disstria*. Entomologia Experimentalis et Applicata 85:161–168.

———. 1998. Host searching and oviposition by *Leschenaultia exul*, a tachinid parasitoid of the forest tent caterpillar, *Malacosoma disstria*. Journal of Insect Behavior 11:583–592.

Murrell, D. J. 2005. Local spatial structure and predator-prey dynamics: counterintuitive effects of prey enrichment. American Naturalist 166:354–367.

Neigh, C. S. R., C. J. Tucker, and J. R. G. Townshend. 2008. North American vegetation dynamics observed with multi-resolution satellite data. Remote Sensing of Environment 112:1749–1772.

Neubert, M. G., and M. Kot. 1992. The subcritical collapse of predator populations in discrete-time predator-prey models. Mathematical Biosciences 110:45–66.

Nicholson, A. J., and V. Bailey. 1935. The balance of animal populations—part 1. Proceedings of the Zoological Society of London 3:551–598.

North, A., and O. Ovaskainen. 2007. Interactions between dispersal, competition, and landscape heterogeneity. Oikos 116:1106–1119.

Peltonen, M., A. M. Liebhold, O. N. Bjornstad, and D. W. Williams. 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. Ecology 83:3120–3129.

Perry, G. L. W., and N. J. Enright. 2006. Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. Progress in Physical Geography 30:47–72.

Pureswaran, D. S., R. Gries, J. H. Borden, and J. Pierce, and D. Harold. 2000. Dynamics of pheromone production and communication in the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae). Chemoecology 10:153–168.

Reeve, J. D., J. T. Cronin, and K. J. Haynes. 2008. Diffusion models for animals in complex landscapes: incorporating heterogeneity among substrates, individuals and edge behaviours. Journal of Animal Ecology 77:898–904.

Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2009. Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s–1930s–2000s). Ecological Applications 19:1061–1078.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559–623.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. Oecologia (Berlin) 93:25–30.

———. 2005. Are the "seeds" of spatial variation in cyclic dynamics apparent in spatially-replicated short time-series? an example from the forest tent caterpillar. Annales Zoologici Fennici 42:397–407.

Roland, J., B. G. Mackey, and B. Cooke. 1998. Effects of climate and forest structure on duration of forest tent caterpillar outbreaks across central Ontario, Canada. Canadian Entomologist 130:703–714.

Roland, J., and P. Taylor. 1995. Herbivore-natural enemy interactions in fragmented and continuous forests. Pages 195–208 *in* N. Cappuccino and P. W. Price, eds. Population dynamics: new approaches and systhesis. Academic Press, San Diego, CA.

———. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386:710–713.

Roth, D., J. Roland, and T. Roslin. 2006. Parasitoids on the loose—experimental lack of support of the parasitoid movement hypothesis. Oikos 115:277–285.

Rothman, L. D., and J. Roland. 1998. Forest fragmentation and colony performance of forest tent caterpillar. Ecography 21:383–391.

Ryall, K. L., and L. Fahrig. 2006. Response of predators to loss and fragmentation of prey habitat: a review of theory. Ecology 87:1086–1093.

Safranyik, L., D. A. Linton, R. Silversides, and L. H. McMullen. 1992. Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. Journal of Applied Entomology 113:441–450.

Schlather, M. 2001. Simulation and analysis of random fields. R News 1:18–20.

Schneider, D. 1992. 100 years of pheromone research—an essay on Lepidoptera. Naturwissenschaften 79:241–250.

Schooley, R. L., and L. C. Branch. 2007. Spatial heterogeneity in habitat quality and cross-scale interactions in metapopulations. Ecosystems 10:846–853.

Seidl, R., P. M. Fernandes, T. F. Fonseca, F. Gillet, A. M. Jonsson, K. Merganicova, S. Netherer, et al. 2011. Modelling natural disturbances in forest ecosystems: a review. Ecological Modelling 222:903–924.

Strohm, S., and R. Tyson. 2009. The effect of habitat fragmentation on cyclic population dynamics: a numerical study. Bulletin of Mathematical Biology 71:1323–1348.

Su, M., C. Hui, Y. Y. Zhang, and Z. Z. Li. 2009. How does the spatial structure of habitat loss affect the eco-epidemic dynamics? Ecological Modelling 220:51–59.

Swift, T. L., and S. J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biological Reviews 85:35–53.

Taylor, P., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Travis, J. M. J., K. Mustin, T. G. Benton, and C. Dytham. 2009. Accelerating invasion rates result from the evolution of density-dependent dispersal. Journal of Theoretical Biology 259:151–158.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Characteristics of insect populations on habitat fragments: a mini review. Ecological Research 17:229–239.

Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Monographs in Population Biology. Princeton University Press, Princeton, NJ.

Turchin, P., S. N. Wood, S. P. Ellner, B. E. Kendall, W. W. Murdoch, A. Fischlin, J. Casas, E. McCauley, and C. J. Briggs. 2003. Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. Ecology 84:1207–1214.

VanKirk, R. W., and M. A. Lewis. 1997. Integrodifference models for persistence in fragmented habitats. Bulletin of Mathematical Biology 59:107–137.

Vepakomma, U., D. Kneeshaw, and B. St-Onge. 2010. Interactions of multiple disturbances in shaping boreal forest dynamics: a spatially explicit analysis using multi-temporal lidar data and high-resolution imagery. Journal of Ecology 98:526–539.

Vet, L. E. M., and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. Annual Review of Entomology 37:141–172.

Wood, D. M., D. Parry, R. D. Yanai, and N. E. Pitel. 2010. Forest fragmentation and duration of forest tent caterpillar (*Malacosoma disstria* Hubner) outbreaks in northern hardwood forests. Forest Ecology and Management 260:1193–1197.

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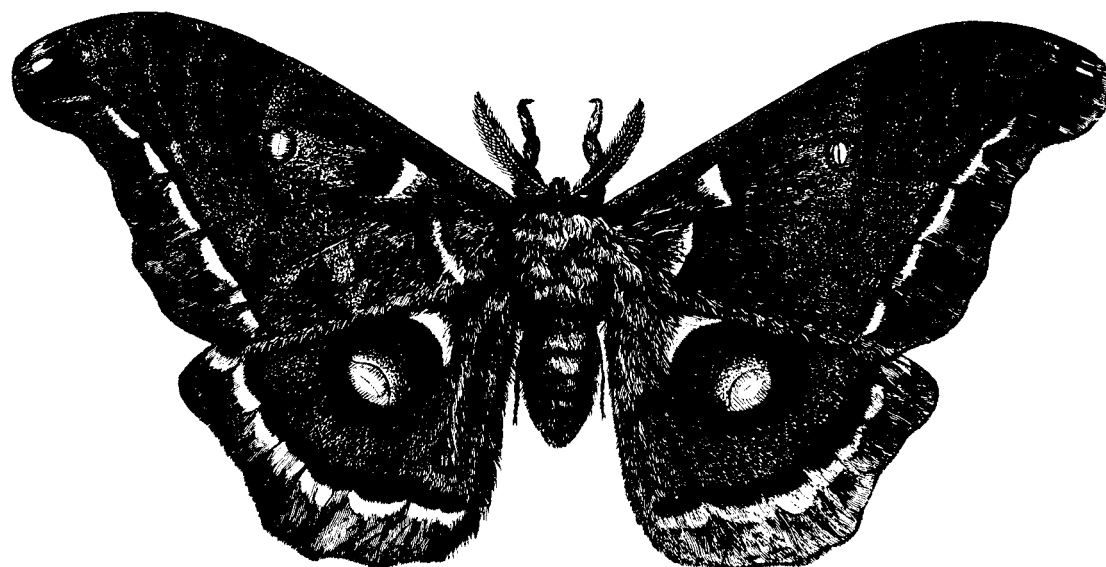
"Having observed how close and air-tight the cocoon of the Polyphemus seems to be, I could not conceive that air was needed for it to breathe. Desirous of ascertaining whether my idea was correct, I took three cocoons, and … I covered them carefully with a thick coating of starch. … After this the cocoons were covered at three different times with a heavy coating of shellac varnish; thus the cocoons were made perfectly air-tight. They were kept in a cold dry room all winter. In July the moths came out perfectly healthy. … So these insects had been nine months with no air, except the very small volume enclosed in the cocoon, and they had accomplished their transformation just as well as if the air had been allowed to come into the cocoon." From "The American Silk Worm (Concluded)" by L. Trouvelot (*The American Naturalist*, 1867, 1:145–149).