Supplement A. The relationship of the proportion of populations that replaced themselves from year t-1 to year t with the respective population density in year t-1 (top graph) demonstrates the presence of both an Allee threshold (~17 moths/trap) and a carrying capacity (~687 moths/trap) in gypsy moth populations. The bottom graph better illustrates this relationship at low densities and more precisely estimates the Allee threshold. We defined the Allee threshold as the moth abundance in year t-1 at which half of the populations replaced themselves in year t, and the carrying capacity threshold as the abundance (in t-1) at which the replacement proportion decreased and dropped below 0.5. These data were gathered from spatially-referenced pheromone-baited trap catches, which were part of the gypsy moth Slow-the-Spread (STS) project (Tobin et al. 2004).

These trap catch data were first used to interpolate male moth abundance using median indicator kriging (Isaaks and Srivastava 1989) over a network of 5×5 km cells in a grid that encompassed the states of West Virginia and Virginia. Interpolated grids were generated for each year from 1996 to 2004. We extracted the interpolated male moth density per trap at the center of each cell, and then paired each interpolated value in year t-1 with its respective value in year t. These pairs of trap counts from successive years (i.e., 1996 to 1997, 1997 to 1998, ... , 2003 to 2004) were then combined to form a single list of all pairs from the entire time interval. We omitted any cells whose value in year t-1 was 0. Also, because some gypsy moth populations are targeted for eradication using chemical or biological pesticides, we excluded any cells that were within 1.5 km from an area treated for gypsy moth control. The final data set contained 20,339 pairs of moth counts in years t-1 and t. For estimation of carrying capacity, we condensed the counts into a series of bins with intervals of 6, (i.e., 1-6 moths, 7-12 moths/trap, etc), though we excluded bins > 700 because of the diminished pheromone trap efficiency that is known to occur as traps become saturated with moths (Elkinton 1987). Within each of these bins, the proportion of cells in which moth abundance either increased or stayed the same between years t-1 and t was calculated. The result was a bivariate relationship between abundance in year t-1and the proportion of cells where populations were replacing themselves (top figure). To pinpoint an estimate of the Allee threshold, we subset the data and used densities in year t-1 that were <30 moths per trap. In this case, the abundances in year t-1 were not placed into population bins; rather, we calculated replacement proportions at each integer density from 1 to 30 male moths/trap (bottom graph).

Estimation of thresholds was done using lowess fits in R (R Development Core Team 2004).

References

Elkinton, J. S. 1987. Changes in efficiency of pheromone-baited milk carton traps as it fills with male gypsy moths (Lepidoptera: Lymantriidae). J. Econ. Entomol. 80: 754-757.

Isaaks, E. H., and R. M. Srivastava. 1989. An introduction to applied geostatistics. Oxford University Press, New York, NY.

Tobin, P. C., A. A. Sharov, A. M. Liebhold, D. S. Leonard, E. A. Roberts, and M. R. Learn. 2004. Management of the gypsy moth through a decision algorithm under the Slow-the-Spread Project. Am. Entomol. 50: 200-209.

R Development Core Team. 2004. http://www.r-project.org.
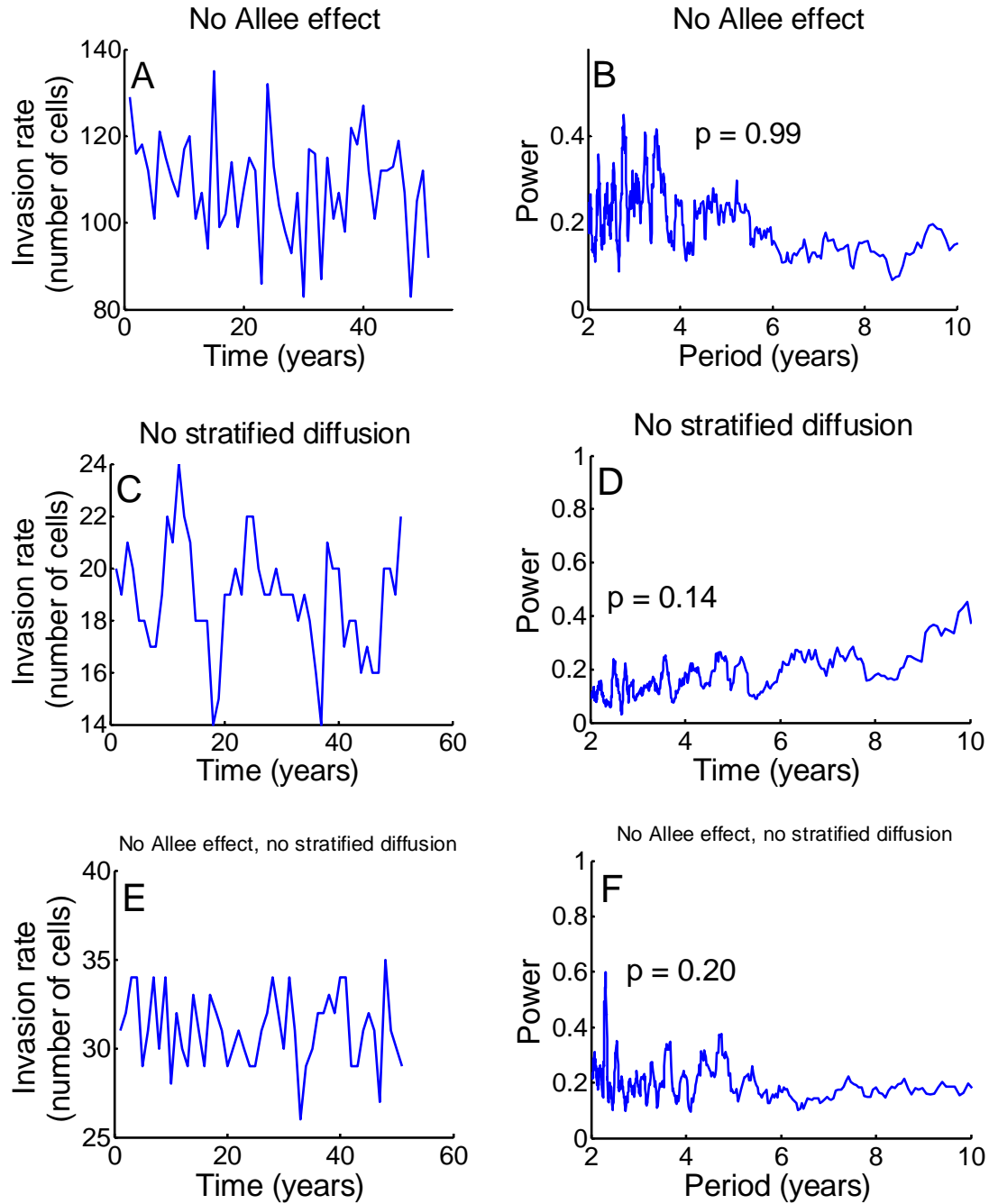
Supplement B. Invasion rates and spectral analyses in simulations of a cyclical

population with a 10-yr periodicity without an Allee effect (Figures A & B), without

stratified diffusion (Figures C & D), and without both (Figures E & F). Invasions were

run in a one dimensional landscape of 1,000 cells. The population size in the first (edge)

cell was initiated at a non-zero value and population sizes in all other patches were initiated at zero. The model used was that presented in the body of the article with the same parameter values, except in the cases where there was no Allee effect ($c = 0$) and/or no stratified diffusion ($\phi = 0$). Significance in the spectrograms were calculated by comparing the maximum power of periodicity in the simulated time series of invasion rates to a distribution of maximum powers of periodicity in 1000 bootstrapped data sets created by resampling the simulated time series with replacement. Invasion rates were not significant at a 95% confidence level in any of the three models; When the Allee effect was excluded ($p = 0.99$), when stratified diffusion was excluded ($p = 0.14$), and when both were excluded ($p = 0.20$). The key observation here is that, in this model, both an Allee effect and stratified diffusion were necessary components to create periodic invasion pulses.
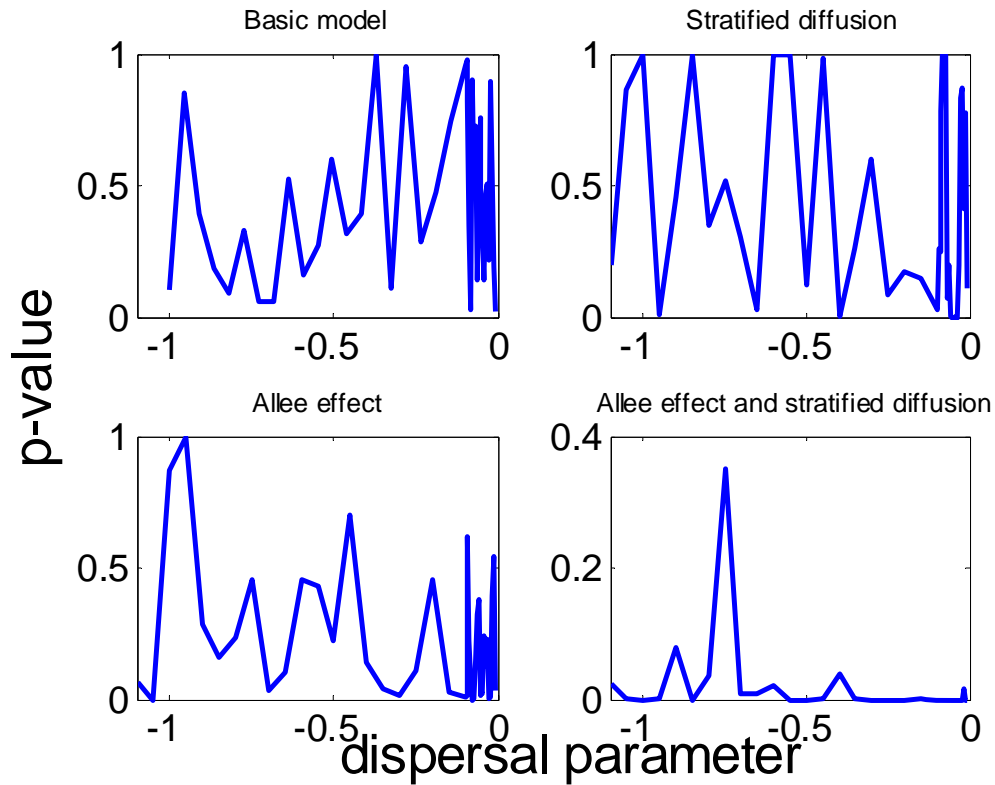
Supplement C. A continuous-space model was approximated by increasing the dispersal parameter (τ) to near zero in the discrete model. Increasing the dispersal parameter (τ) to near zero approximates continuous space because, in effect, it is equivalent to decreasing the scale of cells because they both result in an increase in dispersal distance relative to the number of cells. The purpose of this analysis is to test whether the periodicity, or lack of periodicity, in each of the models is an artifact of using a discrete-space model to model a continuous process. The four models tested were the basic model, the model with stratified diffusion, the model with an Allee effect, and the model with both stratified diffusion and an Allee effect. At the greatest dispersal values, local invasion proceeded at rates of approximately 100 to 200 cells/generation. In all analyses, the mean jump dispersal was held constant at approximately 8 times the local invasion distance. The p-values were calculated by comparing the maximum power of periodicity

of the simulated time series of invasion rates to a distribution of maximum powers of periodicity calculated from 10,000 resamplings of the time series, with replacement, from the simulated time series. While there was high variation in the p-values across values of τ, the significance of periodicity was not a function of τ in any of the models. Periodicity in the model with an Allee effect and stratified diffusion was nearly always significant at $p < 0.05$, while periodicity in the other models were generally not significant across the full range of dispersal values. These results indicate that the observed periodic pulses of invasion are not artifacts of modeling in discrete space.

C=0.01

C=0.1

C=2
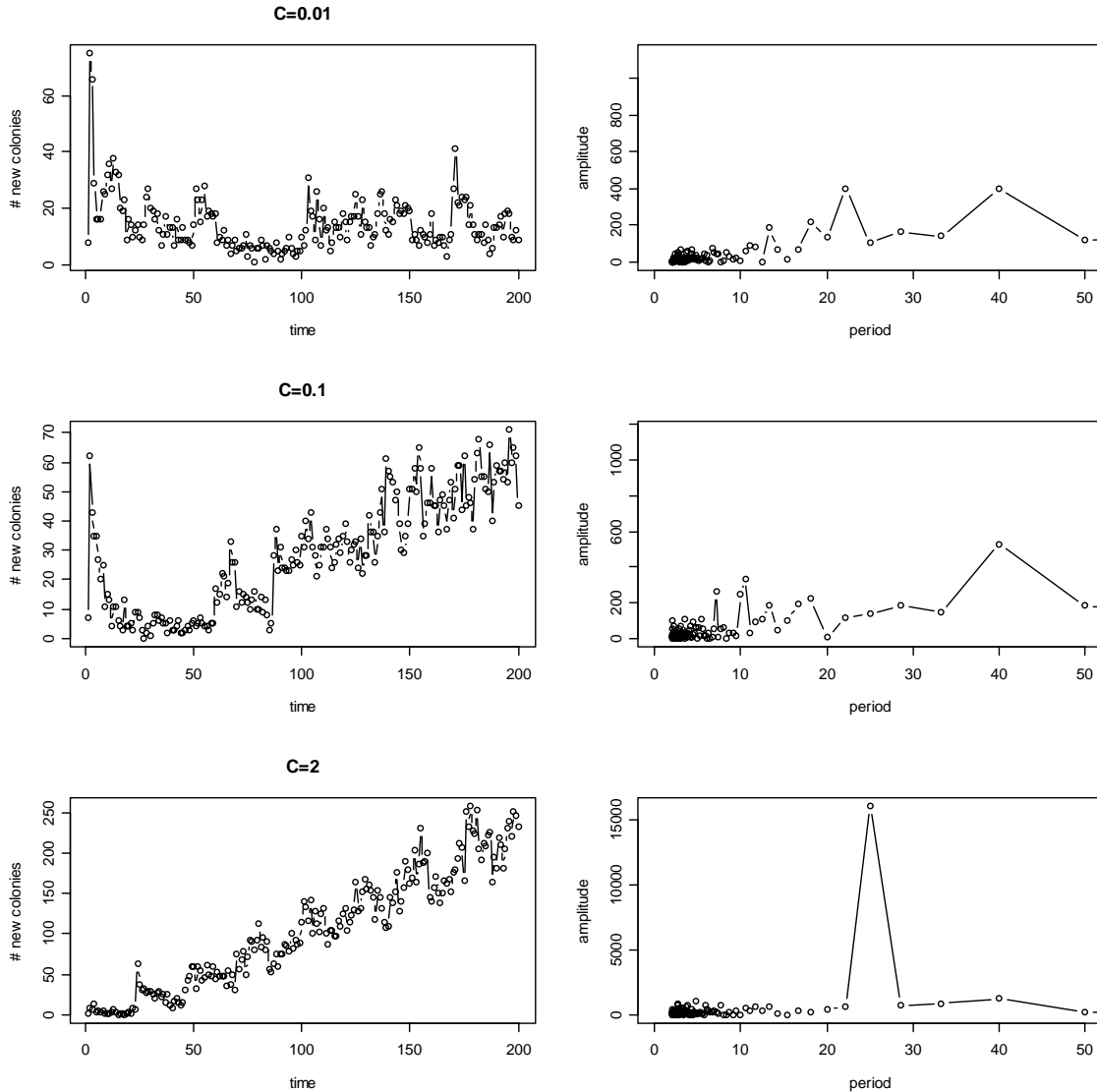
Supplement D. A continuous-space point-process based simulator. The number of new colonies (proxy for invasion rate) against time in the continous-space simulator for three different values of the Allee threshold. Left panels shows the time series, right panels show the associated periodograms. We used a continuous-space point-process simulator to check that our conclusions regarding pulsed invasions and Allee effects also hold in continuous space. Simulating these point-process models was computationally very demanding (simulating 200 generations with a 'basic reproductive ratio' of 10 took 2.5

hours and <20GB of memory), so we were unable to use the full stochastic, Allee'd, log-linear AR-2 model. Instead, we used the simpler deterministic Allee'd logistic model with stochastic spatial dynamics. The determinism with respect to local growth gave reasonable precision on the basis of single replicate simulations.

The local colony growth was according to Liebhold and Bascompte's (2003) model:

$$N_{i,t} = N_{i,t-1}e^{\left(r\left(1-\frac{N_{i,t-1}}{K}\right)\left(\frac{N_{i,t-1}-C}{K}\right)\right)},$$

where C is the Allee threshold and K is the carrying capacity. We started with a single colony at the origin. Each colony was assumed to give rise to a Poisson number of 'offspring' colonies (arbitrarily set to have expectation 10) that were initiated with a fraction d of the parent's abundance. Each is seeded at a new location away from the parent according to a diffusion process (i.e. 2D Gaussian kernel with scale d_a) that we took to represent the long-distance dispersal of the stratified diffusion; local dispersal is, here, subsumed in the local population growth. Colony initiation success depends on local density of colonies (so that there can't be an infinite number of colonies in an infinitely small area; this is essentially equivalent of 'space-filling') according to a Gaussian 'competition' kernel, κ, with some scale, d_c. The rate of 'competition for space' at a candidate location j is $m_j = \theta \int_{k \in \Omega} \kappa(|j-k|)$, where $|j-k|$ is the distance between location j and a previously established colony k, so that the probability of successful initiation is $1-e^{-m_j}$.

The simulation is run with growth followed by colony seeding (i.e. discrete time but continuous space), and with parameters arbitrarily fixed at r = 1.5, K = 100, d_a = 10,

$d_c = 2$, $\theta = 10$ and C varying between 0.01 (virtually no Allee effect) to 2 (very high Allee threshold). A sensitivity analysis with respect to the growth rate revealed a trivial effect (higher growth yields faster pulses) for low values of r (the discrete logistic bifurcates at r >2.5). All simulations result in an essentially exponential growth of the number of colonies. The following figures show the number of successful new colonies through time (the proxy for range expansion) for the range in Allee threshold with associated spectra: Conspicuous pulses appear as the Allee threshold increases. We conclude that the pulses in the gypsy moth lattice model are not an artifact of the discretization of space.

Reference

Liebhold, A. & J. Bascompte. 2003. The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters* 6(2): 133-140.
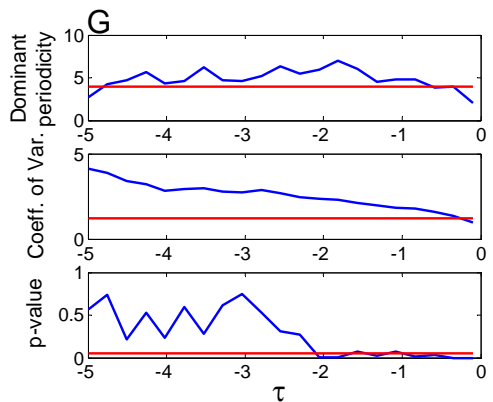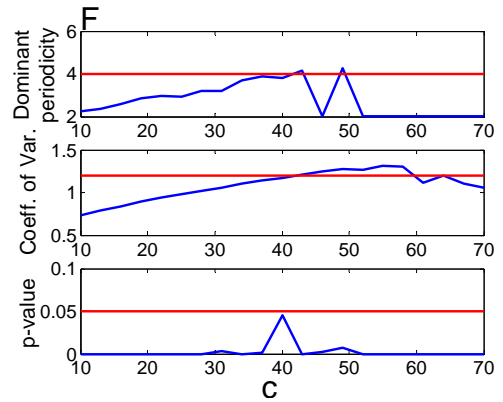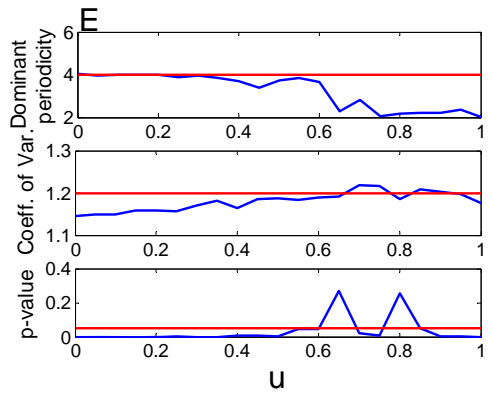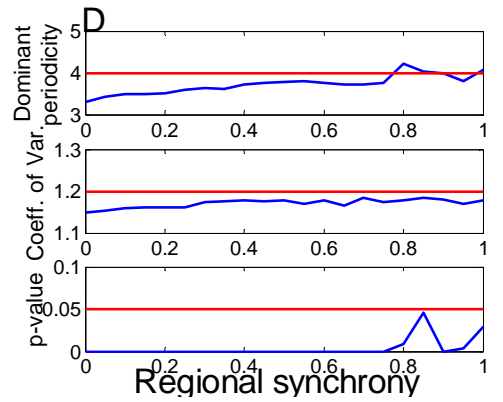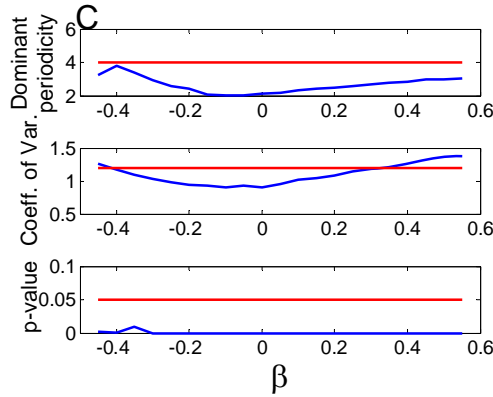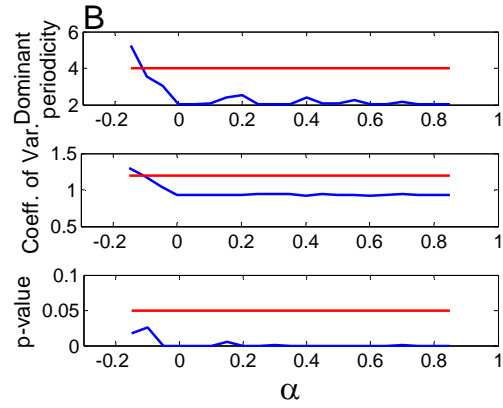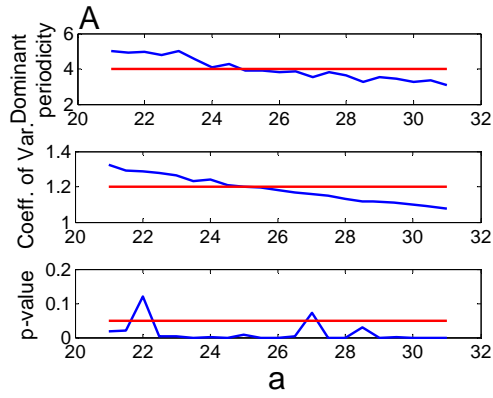
Supplement E. Sensitivity analysis of the effects of variation in model parameters to

length, coefficients of variance, and significance of periodicity in invasion pulses. The

coefficient of variance is indicative of the magnitude of invasion pulses independent of

scale of the discrete model. In each set of three graphs, horizontal red lines in the first

two graphs indicate the periodicity and coefficient of variance observed in the gypsy

moth data illustrated in Figure 3 of the article, and indicates a p-value of 0.05 in the third

graph. Methods were the same as those used for analyses illustrated in Figure 4. With

the exception of the exponential dispersal parameter (τ) (Figure G), periodicity over most

of the parameter ranges was significant at $p < 0.05$, indicating that periodicity in invasion

pulses in the model is robust to variation in parameters. All measures of periodicity

varied somewhat due to stochasticity (u) in the model (except for when $u = 0$ in Figure

E). Increasing the value of the population growth parameter (a) from 21 to 31 resulted in

a decrease in the periodicity and coefficient of variance of invasion pulses (Figure A). In

the sensitivity analysis, the first-order density-dependence parameter (α) was varied from

-0.15 to 0.85. As α was increased from -0.15, the dominant periodicity and coefficient of

variance rapidly decreased from approximately 6 years to near 2 years at $\alpha = 0$. Between

α values of 0 and 0.85, neither the dominant periodicity and coefficient of variance

showed any apparent trend. Periodicity was not significant at α values below -0.15. The

rate of invasion is clearly affected by interactions between factors, thus, these sensitivity

analyses do not suggest that, for example, a certain value for α will always result in a

given periodicity of invasion. Instead, a given combination of parameters results in

specific model dynamics. So, with values of $\alpha < $ -0.15, we could possibly vary other

parameters in the model to allow invasion to occur. However, doing this for all parameters would entail a sensitivity analysis in 7 dimensions of parameter space, which is beyond the scope of this project. Pulses were not periodic for values of the second-order density-dependent parameter $\beta < -0.5$. As β was increased from -0.4 to -0.1, the dominant periodicity decreased from approximately 4 years to 2 years, and the coefficient of variance decreased (Figure C). Between β values of -0.1 and 0.55, the dominant periodicity increased up to approximately 3.5 years and the coefficient of variance increased as well. Periodicity increases from approximately 3.3 years to 4 years and the coefficient of variance increased moderately as regional synchrony was increased from a proportion of 0 to 1 (Figure D). An increase in stochasticity (u) from 0 to 1 resulted in a decrease in dominant periodicity from 4 years to approximately 2 years and an increase in the coefficient of variance (Figure E). When the model lacks stochasticity ($u = 0$) the populations do not cycle – instead settling at carrying capacity – yet periodic invasion pulses remain, illustrating that population cycles are not a necessary ingredient in pulsed invasion dynamics. Increasing the value of the Allee threshold parameter (c) from 10 to 42 caused a linear increase in dominant periodicity from 2 to 4 years and a corresponding increase in the coefficient of variance (Figure F). Between $c = 42$ to 52, variation in the estimation of dominant periodicity fluctuated between 2 and 4 years and the coefficient of variance leveled off. Between $c = 52$ to 70, the dominant periodicity was at 2 years and the coefficient of variance decreased slightly. The sensitivity of periodicity in pulses of invasion to variation in dispersal was tested between dispersal parameter values between $\tau = -5$ and -0.1. Periodicities were only significant for values of $\tau = -2$. As τ was increased from -2 to -0.01, the dominant periodicity decreased from approximately 7.5 to

3 years and the coefficient of variance also decreased. In summary, the periodic pulses of invasion are robust to moderate variation in model parameters.