Popul Ecol (2008) 50:379–389
DOI 10.1007/s10144-008-0105-5

SPECIAL FEATURE: ORIGINAL ARTICLE

Spatial Population Synchrony

Transient synchronization following invasion: revisiting Moran's model and a case study

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Received: 12 February 2008 / Accepted: 9 July 2008 / Published online: 5 August 2008

Abstract Synchrony in forest insect outbreaks is important because the resulting regionalized outbreak dilutes the regulating effects of natural enemies, reduces the landscape's ability to buffer the disturbance, exacerbates the economic burden on individual stakeholders, and overwhelms the logistical abilities of managers to suppress populations and mitigate impacts. Understanding the process of synchronization of dynamics is therefore a crucial aspect of understanding outbreak dynamics. We studied the second-order log-linear (autoregressive) model to ask what patterns of synchronization across invasion fronts may be expected from Moran's model. Generally, we show that the time to synchronization in the log-linear model is a complex function of a number of parameters of which the overall strength of regulation, the strength of delayed statistical density dependence, and the relaxation time seem to be of particular importance. Interestingly, while environmental correlation is the crucial determinant of the magnitude of asymptotic synchrony, it does not appear to influence the transient process of synchronization. However, synchronization proceeds much more quickly among weakly periodic populations than among populations that are strongly periodic. As a case study, we investigate synchronization following colonization by gypsy moth (*Lymantria dispar*) populations located along the species's expanding invasion front in northeastern USA. Data consisted of more than 100 years of county quarantine records and 30 years of detailed defoliation maps. We found that the dynamics of new populations tended to be initially out of synch with the broadly synchronized outbreaks within the established range. However, the outbreak dynamics of these new populations lock on to the regional patterns very quickly—within 10–15 years of invasion. Focusing on parameters that produce periodicity comparable to that seen in real gypsy moth populations, we discuss how the observed synchronization compares to that predicted by the log-linear model. While our results are equivocal, the synchronization appears to be surprisingly rapid, so more mechanistic models may be needed to explain the synchronization observed in this case study.

Keywords Autoregressive model · Defoliation · Gypsy moth, *Lymantria dispar* · Moran effect · Spatiotemporal population dynamics · Transient dynamics

Introduction

Populations of most forest insect herbivores persist at low densities such that they are rarely noticed. In contrast, a few species of foliage-feeding lepidopterans exhibit extreme variability in abundance. During years of high abundance, individual host trees may be completely defoliated, and this often leads to reduced growth and tree

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This manuscript was submitted for the special feature based on the symposium in Jozankei, Hokkaido, held on 21 October 2007.

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mortality. Of these outbreaking species, a handful are responsible for some of the most expansive and intense disturbances of forests worldwide. The manifold consequences of these outbreaks include alteration of nutrient cycles and shifts in animal/plant community structure (Payette et al. 2000; Work and McCullough 2000) as well as impacts on human utilization of forests for timber, recreation, and aesthetics (Volney 1998; Coyle et al. 2005).

There are two main reasons why these outbreaking species are such important pests. First is their ability to reach very high densities that cause considerable damage to individual host trees. This is a property that has, throughout the history of ecology, received in-depth attention and has revealed fundamental insights into pest biology and dynamics. The second reason is that their population peaks are geographically synchronized, resulting in regionalized outbreaks. This spatial synchrony is crucial for at least four reasons. First, it dilutes the regulating effects of any natural enemy that could otherwise provide local control. Second, it reduces the ecological landscape's ability to buffer because most areas within a watershed or greater ecosystem will experience simultaneous disturbance (Lovett et al. 2002). Third, it greatly exacerbates the economic burden on individual stakeholders because a majority of his/her tract of land may be damaged during any given outbreak. Finally, the massive geographical scale of the outbreaks—for example the 65 million cumulative acres defoliated by the gypsy moth over the last 25 years—vastly overwhelms the budgetary and logistical abilities of government agencies to suppress populations and thereby mitigate impacts. Synchronization of dynamics is therefore a key determinant of the ecological and economic impacts of forest defoliating insects.

"Spatial synchrony" refers to the statistical congruence in the oscillations of geographically disjunct populations. This phenomenon has received considerable recent attention in population ecology because spatial synchrony has been found to be ubiquitous across animal populations (reviewed in Bjørnstad et al. 1999a; Liebhold et al. 2004a). Current theory explores two broad classes of mechanisms for spatial synchronization. The first centers on how patterns of dispersal in either the focal population or its natural enemies can cause synchrony. The second centers on how even modest but regionalized stochastic perturbations—such as variable weather and climatic shocks or region-wide trophic effects (e.g., mast-seeding effects on the food supply of seed-eating insects)—may synchronize population fluctuations. This second mechanism has received prominence in the ecological literature as the "Moran effect" (Royama 1992; Ranta et al. 1997; Bjørnstad et al. 1999a; Johnson et al. 2004) named after Moran's (1953a, b) prescient study of how random but spatially correlated stochastic forcing may synchronize fluctuating populations. Moran's theorem (Royama 1992) details how any two spatially disjunct populations governed by identical linear or log-linear density-dependent feedbacks will directly inherit their synchrony from the correlation in the environment. Moran (1953a, b) derived this result from studying a second-order autoregressive model fit to the time series of Canadian lynx log-abundance. An important conceptual insight from Moran's work is that the cause of synchronization can be different from the causes responsible for the oscillations.

A principal reason for the difficulty in deducing the causes of synchrony is that most forest insect populations are already synchronized and thus the actual process of synchronization can rarely be observed. An exception to this may be during invasions of alien populations when newly founded populations may be initialized out of synch with previously established populations (Johnson et al. 2006b). Such invasions may therefore offer insights into synchronization and regionalization of outbreaks. In this paper, we first use the second-order log-linear model to study how direct density dependence and delayed density dependence affect the speed of synchronization along invasion fronts. We show that local regulatory processes are important determinants of the speed of regionalization of outbreaks despite the fact that (in linear and log-linear systems) long-term synchrony is independent of these. We then discuss an empirical analysis of the initial asynchrony and subsequent rapid synchronization of populations along the gypsy moth invasion front in the northeastern US. For this case study, we speculate that nonlinearities in the local dynamics may also be important for the observed rapid synchronization.

Theoretical explorations

Most empirical studies of synchrony—including our own various efforts (e.g., Bjørnstad et al. 1999b; Bjørnstad 2000; Williams and Liebhold 2000; Peltonen et al. 2002)—focus on populations that are in their "asymptotic mode" of dynamics (i.e., stochastically fluctuating around the carrying capacity or cyclic/chaotic attractors). Following Moran's (1953a) study we know that in (log-)linear dynamical systems, this asymptotic rate of synchrony is determined by the strength of spatial coupling and is independent of local dynamics. Here we ask whether and how the *rate of synchronization* depends on local dynamics. To investigate this we use the second-order autoregressive (AR2) model of log-abundance as the benchmark. This model has been used in the study of synchrony, beginning with the work of Moran (1953b) but continued in several other studies (Royama 1992; Peltonen et al. 2002; Liebhold et al. 2006), and has in specific case studies been derived as a useful approximation to more mechanistic models of trophic interactions (e.g., Stenseth et al. 1996, 1998). The AR2 model for abundance (n) in population i in year t is:

$$n_{i,t} = ce^{\varepsilon_{i,t}} n_{i,\,t-1} n_{i,t-1}^{\alpha} n_{i,\,t-2}^{\beta}, \tag{1}$$

where c is the maximum population growth rate, α and β are the coefficients of direct and delayed density dependence, and ε_i is a sequence of zero-mean, identically distributed random normal deviates with variance σ^2. On a log-scale, Eq. 1 can be written in the standard autoregressive form as:

$$x_{i,\,t} = c' + a_1 x_{i,\,t-1} + a_2 x_{i,\,t-2} + \varepsilon_{i,\,t}, \tag{2}$$

where $x_{i,\,t} = \log(n_{i,\,t})$, $c' = \log(c)$, $a_1 = 1 + \alpha$, and $a_2 = \beta$.

Dynamically speaking, this model has been fully characterized in the statistical (e.g., Priestley 1981) and dynamical systems (e.g., Honerkamp 1993) literature. For our discussion it is useful to summarize some key results from this literature. In the absence of stochasticity, this model exhibits dampened or divergent dynamics around the equilibrium, $\bar{x} = c'/(1 - a_1 - a_2)$. In the parameter region where $a_2 > -1$ and $a_1^2 + 4a_2 < 0$, the dynamics is represented by dampened oscillations with a period, T, that is to a first order of approximation $2\pi\Big/\cos^{-1}\left(\frac{a_1}{2\sqrt{-a_2}}\right)$ (Fig. 1a). In this region, the so-called relaxation time towards the equilibrium is $\tau = -2/\log(-a_2)$ (Fig. 1b). This relaxation time measures the time it takes for displacements away from $\bar{x}$ to decay by about 63% (i.e., to a fraction $1 - e^{-1}$ of the original displacement). This, therefore, is a measure of how long any particular shock will influence the dynamics. Note that this parameter depends only on the magnitude of the delayed density dependence and not on the direct density dependence. The two eigenvalues of the system are $\lambda = (a_1 \pm \sqrt{a_1^2 + 4a_2})/2$ (Fig. 1c). In the presence of white-noise stochasticity (i.e., $\sigma^2 > 0$), the model exhibits persistent oscillations with a statistical period approximately equal to T. The autocorrelation function at time lag l takes the form

$$acf(l) = \frac{\operatorname{sign}(a_1)^l d^l \sin(p * l + f)}{\sin(f)}, \tag{3}$$

where $d = \sqrt{-a_2}$, $p = \cos^{-1}(\operatorname{abs}(a_1)/2d)$, and $f = \tan^{-1}(\tan(p)(1 + d^2)/(1 - d^2))$. The theoretical spectrum is

$$h(\omega) = \left(2\pi|1 - a_1 e^{-2\pi\omega i} - a_2 e^{-4\pi\omega i}|^2\right)^{-1}, \tag{4}$$

where ω is the frequency (=1/period), i is the imaginary unit, and || is the complex modulus.

To study time to synchronization, we consider a simple two-patch system ($i \in \{1, 2\}$) where the dynamics are identical except for the stochastic forcing being partially correlated: $\mathrm{Cor}(\varepsilon_1, \varepsilon_2) = \rho$. Consequently, the asymptotic correlation in abundance, $\mathrm{Cor}(x_1, x_2)$, is also ρ (Moran 1953a; Royama 1992). We characterize the process of synchronization by investigating how the 10-year moving-window correlation (e.g., Ranta et al. 1997) changes as a function of time and measure the time to synchronization as the average time it takes to reach the asymptotical correlation.

To make it as applicable as possible to our gypsy moth case study (see below), we assume the maximum annual

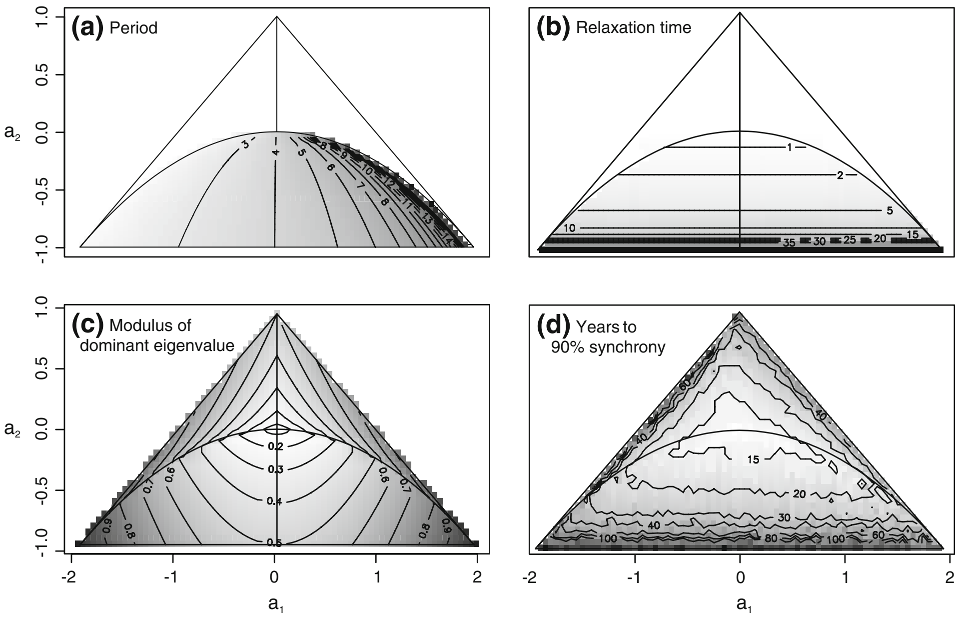

Fig. 1 **a** Damping period as a function of direct (a_1) and delayed (a_2) coefficients of density dependence. The *triangle* represents the stable (nondivergent) region of parameter space. The *parabola* demarcates the region where stochastic dynamics are statistically periodic. *Contours* represent cycle period. **b** Relaxation time. **c** The modulus of the dominant eigenvalue. **d** The time to reach 90% asymptotic synchrony (for $\rho = 0.8$ and $\sigma = 1$)

per capita growth ratio to be around 50 (Elkinton et al. 1996) giving $c' = 4$. Since the new populations in front of an invasion front are generally seeded at low abundance when populations in the established populations are at high abundance (Johnson et al. 2006b), we initiate our populations using the observed peak-to-trough ratio observed in gypsy moth time series. Liebhold et al. (1998) report somewhere between a 1,000-fold and a 10,000-fold difference across a cycle. We consequently set $x_{1,t=0} = \bar{x} + 4$ and $x_{2,t=0} = \bar{x} - 4$, which correspond to an approximately 3,000-fold difference. Note that all our results are qualitatively robust to these parametric choices. We explore the time to synchronization across the convergent part of the AR2 parameter space (i.e., where $|\lambda| < 1$) and investigate how this correlates with the basic (a_1, a_2, σ^2, and ρ) and emergent (T, τ, and λ) parameters. Because time to synchronization is slow for certain parameter sets, we also use a relaxed measure of time to synchronization as 90% of the asymptotically expected correlation (ρ). We present averages across 100 replicate simulations of 500 generations for each parameter set. The values of parameters a_1 and a_2 were divided into increments of 0.05 within the convergent part of the parameter space, σ equalled 0.5, 1 or 2, and ρ 0.2, 0.4, 0.6 or 0.8.

Results

The time to synchronization varied from virtually instantaneous (i.e., by the first 10-year moving window) to very slow. Of the 19,752 parameter sets we investigated, 3% reached asymptotic synchrony within 15 generations, nearly 10% took longer than 500 generations, 10% took between 100 and 500 generations, and around 75% took between 15 and 100 years. This qualitative pattern remained the same when we used the less stringent criterion of reaching 90% of asymptotic synchrony. In the remainder of our exploration, we will focus on this less stringent criterion.

A cursory inspection suggests that time to synchronization decreases to a greater or lesser extent with all the basic parameters: the Spearman rank correlations with a_1, a_2, σ, and ρ are -0.14, -0.53, -0.24, and -0.10, respectively. However, a closer inspection reveals these relationships to be complicated with obvious interactions among the parameters (Fig. 1d). Generally, time to synchronization is shorter when $\{a_1$ and $a_2\}$ are close to the origin and the noise variance is large, and longer when $\{a_1$ and $a_2\}$ are closer to the boundary of instability, particularly so when a_2 is very negative. This generalization is supported by the analysis of variance of (log-transformed) time to synchronization, for which the absolute value of the dominant eigenvalue, $|\lambda|$, was positively related to the time with a partial $R^2 = 0.21$, followed by a_2 (partial $R^2 = 0.19$), σ (partial $R^2 = 0.05$), a_1 (partial $R^2 = 0.02$), and ρ (partial $R^2 < 0.01$). However, the determinants of time to synchronization are only partially resolved by this analysis as the total R^2 is only 0.48, and while several interactions between the variables are "significant,"[1] even including all interactions up to the full five-way model (with 26 additional parameters) only increases the R^2 to 0.50.

Only considering the nonperiodic region (above the parabola in Fig. 1), the proximity to the boundary of instability (i.e., $|\lambda|$) accounts for 49% of the variation with minor contributions by the other variables: a_2 (partial $R^2 < 0.01$), σ (partial $R^2 = 0.07$), a_1 (partial $R^2 = 0.06$), and ρ (partial $R^2 < 0.01$).

The separate analysis of the parameter region of statistical periodicity (below the parabola in Fig. 1) offers some additional insights. In this region we can investigate how the time to synchronization also correlates with the period, T, and the relaxation time, τ. In this region, the crude Spearman rank correlations of time to synchronization in this region are as follows: with a_1, -0.13; with a_2, -0.86; with σ, -0.20; with ρ, -0.09; with $|\lambda|$, 0.62; with T, -0.13; and with τ, 0.86. Note that τ and a_2 represent negative but inverse transformations of each other so their rank correlations are identical but of opposite sign. The analysis of variance shows that of these, a_2, $|\lambda|$, and τ account for a partial R^2 of 0.72. There is such strong colinearity among these parameters that it is difficult to apportion contributions, but the drop-one ranking puts their importance as $\tau > a_2 > |\lambda|$. The ranking of the remaining variables is σ (partial $R^2 = 0.04$), a_1 (partial $R^2 = 0.01$), ρ (partial $R^2 < 0.01$), and T (partial $R^2 < 0.01$).

In summary, the time to synchronization in the log-linear autoregressive model is a complex function of a number of parameters of which the overall strength of regulation (inversely proportional to $|\lambda|$), the strength of delayed statistical density dependence (a_2), and/or the relaxation time (τ) seem to be of particular importance. Interestingly, while environmental correlation (ρ) is the crucial determinant of the asymptotic synchrony (cf. Moran's theorem), it does not appear to influence the transient process of synchronization. Moreover, the magnitude of the noise variance (σ) and the exact periodicity of the oscillations (T) appear to be unimportant in this process. Finally, the strength of statistical density dependence (a_1) only influences the time to synchronization in so far as it influences the overall strength of regulation ($\propto 1/|\lambda|$).

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[1] We note here that the notion of statistical significance is, obviously, not relevant in this kind of simulation study because one can always find "$P < 0.05$" if the sample size is increased sufficiently.

Gypsy moth as a case study

Basic biology

The gypsy moth, *Lymantria dispar*, is an excellent model system for investigating space-time patterns in pest outbreaks because this species has been the subject of a great deal of research, and considerable information exists on its population biology. While the gypsy moth is alien in North America, having been introduced around 1869, it is also a pest species in much of its native range in Europe and Asia (Giese and Schneider 1979). Throughout the world, populations are known to oscillate with either ~5- or ~10-year population cycles (Williams and Liebhold 1995; Johnson et al. 2006a).

As with most cyclic forest insects, the mechanisms that cause gypsy moth population oscillations are not completely understood, but a lot is known. High-density populations can be strongly influenced by density-dependent epizootics that typically cause outbreak populations to collapse. These epizootics are dominantly caused by two pathogens: the *Lymatria dispar* nucleopolyhedrosis virus (LdNPV) (Dwyer and Elkinton 1993) and the fungal pathogen *Entomophaga maimaiga* (Hajek 1999). In some cases, specialist parasitoids may also contribute to the collapse (Williams et al. 1992). Low-density populations are most strongly affected by generalist predators, especially small mammals (Bess 1961; Campbell and Sloan 1977; Elkinton et al. 1996; Jones et al. 1998). Though voles are known to prey on gypsy moths, most predation is typically caused by the deer mouse and its congeners, *Peromyscus* spp. (Smith 1981). Predation by small mammals is generally the largest source of mortality in low-density populations, but gypsy moths represent a small proportion of the diet of these predators, and there is apparently no numerical response to gypsy moth densities (Elkinton et al. 2004; Schauber et al. 2004). Changes in low-density gypsy moth populations are inversely correlated with small mammal densities (Elkinton et al. 1996; Grushecky et al. 1998).

Despite high levels of strongly density-dependent disease mortality, there is little evidence that the pathogens alone are capable of producing the observed gypsy moth population cycles (Dwyer et al. 2004). Parasitism alone is also unlikely to generate the cycles because rates of parasitism by specialist parasitoids are generally low and parasitism rates do not tend to closely track changes in population density (Elkinton and Liebhold 1990; Ferguson et al. 1994). Recently, Dwyer et al. (2004) proposed a model that showed that the combined effect of LdNPV and predation by small mammals is capable of generating 10-year cycles. This model quantifies the relatively robust hypothesis that has been advanced by several research groups (Elkinton et al. 1996; Jones et al. 1998; Liebhold et al. 2000).

Another convenient aspect of the North American gypsy moth as a model system is that the moths are not very mobile. Adult females are incapable of flight and consequently oviposit within meters of where they fed as larvae (Lance et al. 1987). Hence, passive windborne movement of ballooning first instars is the primary mode of dispersal (Mason and McManus 1981). This means that gypsy moth dispersal is likely to be a relatively unimportant contributor to observed patterns of synchrony. A further consequence of this low mobility is that the invasion of North America has occurred over an extended period of time, during which massive amounts of data have been collected. The gypsy moth was accidentally introduced near Boston around 1869 and has been spreading at a very slow rate of 3–25 km/year since 1900 (Liebhold et al. 1992; Tobin and Whitmire 2005). Gypsy moth spread is dominated by a “stratified diffusion” process in which occasional long-distance dispersal occurs through the accidental movement of life stages coupled with continuous short-distance windborne dispersal of first instars (Sharov and Liebhold 1998). The result is a pattern in which isolated populations are founded ahead of the expanding population front. These colonies slowly expand and ultimately coalesce with the continuously expanding population. Moreover, because of strong Allee effects (Tobin et al. 2007), invasions tend to occur in a pulsed fashion (Johnson et al. 2006b).

Empirical patterns: initial asynchrony and rapid synchronization

In order to investigate the synchronization of populations following invasion, we analyzed time series of gypsy moth populations that became established along the expanding population front at various times during the particularly data-rich recent period (post-1975) for which annual defoliation maps exist. Our first step in generating these time series was to delineate geographical areas in a GIS according to their invasion history, based upon county-level quarantine records (Fig. 2). These data record the year that each county was designated as quarantined (based upon establishment of gypsy moth populations) by the US Department of Agriculture (USDA) and recorded in the US Code of Federal Regulations, Title 7, Chapter III, Sect. 301.45–3. We subsequently grouped counties into those invaded prior to 1975 vs. those invaded in subsequent 5-year periods (1980–1984, 1985–1989, 1990–1994, 1995–1999, 2000–2004) and thereby delineated five regions, identified here as “invasion cohorts” (Fig. 2). No counties were quarantined between 1975 and 1979. Our dataset, therefore, consists of five invasion cohorts. Because spatial synchrony approaches zero among gypsy moth populations

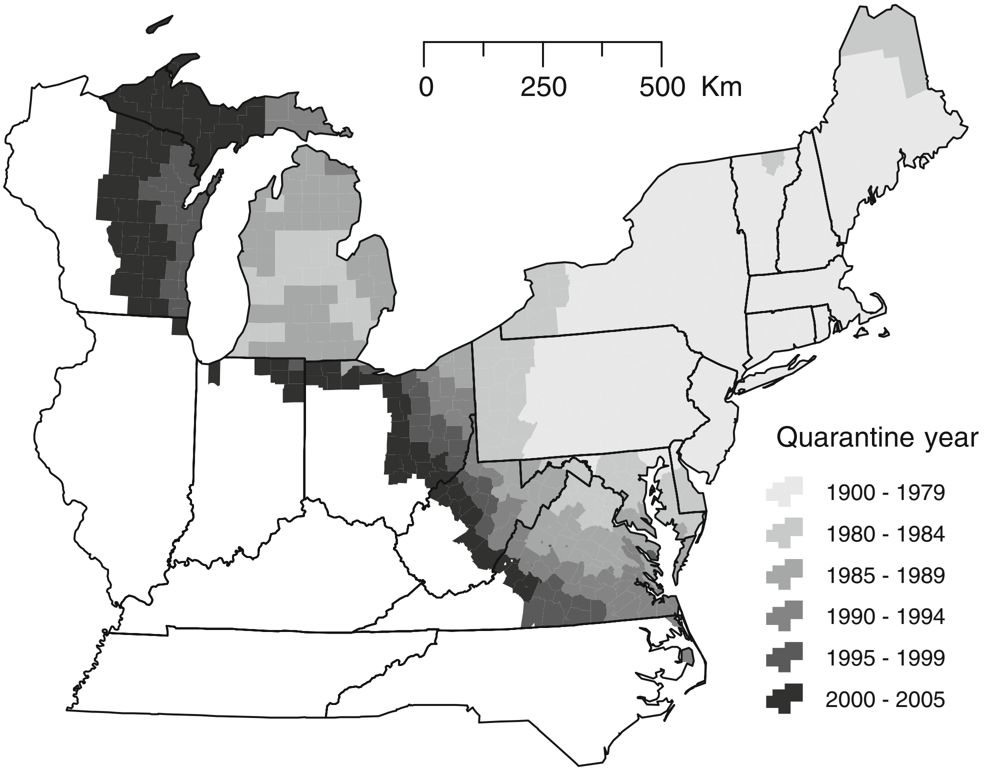

Fig. 2 Gypsy moth range according to their invasion history based on historical county-level quarantine records

separated by >800 km (Peltonen et al. 2002), we excluded the data from the distantly located counties in Michigan, western Ohio, Illinois, Indiana and Wisconsin.

The second step was to generate defoliation time series for each invasion cohort by extracting annual levels of defoliation. Historical maps of gypsy moth defoliation were compiled from aerial surveys from 1974 to 2005 and digitized as a raster layer (2 × 2 km) in a GIS (Liebhold et al. 1997). Time series were compiled by summing the total area defoliated annually in each invasion cohort. The use of defoliation data as a proxy for abundance is obviously prone to significant measurement error. Particularly, this proxy is insensitive at low gypsy moth densities. However, there are numerous previous studies that document a statistical association between gypsy moth density (measured by counts of egg masses per hectare) and defoliation both in time and space (reviewed in Johnson et al. 2006a). Similarly, an aggregate time series was compiled for the area where the gypsy moth was already established by 1975 (Fig. 3). We call the latter the "great attractor." The overall propensity for outbreaks every 10 years (with a tendency towards a subdominant 5-year super-harmonic) is readily visible in the aggregate time series (see Johnson et al. 2006a for a detailed analysis of this cyclicity).

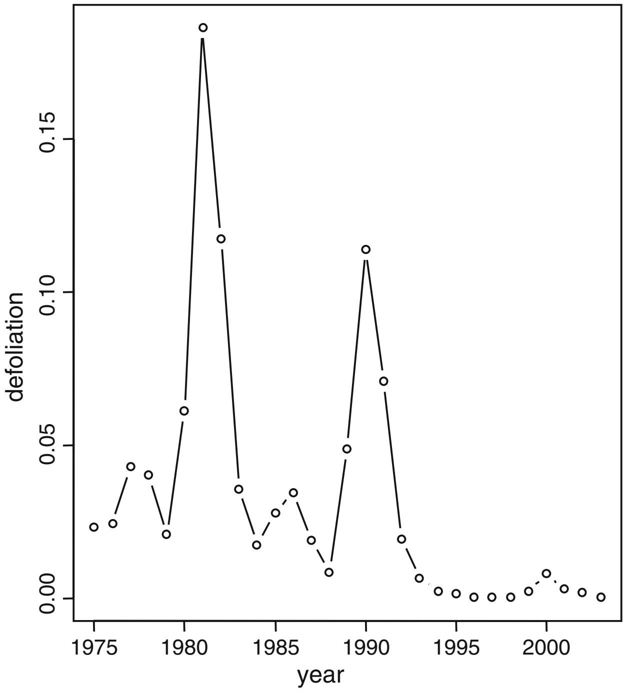

Fig. 3 Aggregate defoliation time series as a proportion of total area for the region where the gypsy moth was established prior to 1975 but excluding counties in Michigan, western Ohio, Illinois, Indiana, and Wisconsin

To estimate synchrony and changes in synchrony through time, we subsequently calculated the correlation between the time series from each invasion cohort with the "great attractor" using a moving 10-year window. We characterize the synchronization process by investigating how this moving-window correlation changes as a function of time since initial invasion (measured by the date of quarantine). To quantify the background level of synchrony within the area invaded prior to 1975, we also undertook the same moving-window analysis for all 5-year quarantine cohorts colonized between 1900 and 1970. So as not to bias the estimate of synchrony for these earlier cohorts, we calculated these correlations against aggregate time series from which the cohort in focus had been removed.

Overall there was a high level of outbreak synchrony among populations within the established range. The average correlation between each 5-year cohort and the great attractor (with that particular cohort removed) was 0.81 [interquartile range (IQR): 0.76–0.93] (Fig. 4). In contrast, among the 1975–2004 invasion cohorts, gypsy moth outbreaks immediately following invasion tended to be out of sync (or even somewhat "anti-synchronous") with regionalized outbreaks in the established range (Fig. 4). For example, the initial correlations between the 1985 and 1995 cohorts and the great attractor were –0.04 and −0.27, respectively. Remarkably, despite the initial asynchrony, all new populations appear to lock on to the regional great attractor within about 10–15 years (Fig. 4). A smooth-spline fit of correlation against time-since-quarantine reached the regional average by year 11 post-invasion (for which the 10-year moving-window is centered on year 16). A sensitivity analysis of our results relative to the moving-window width showed that our results are robust to the size of the moving window. For example when we use a 15-year window, the average correlation within the established range is then 0.80 (IQR: 0.79–0.93), and the initial correlation of the 1985 cohort is 0.06. The time series for the 1995 cohort is too short to provide an estimate.

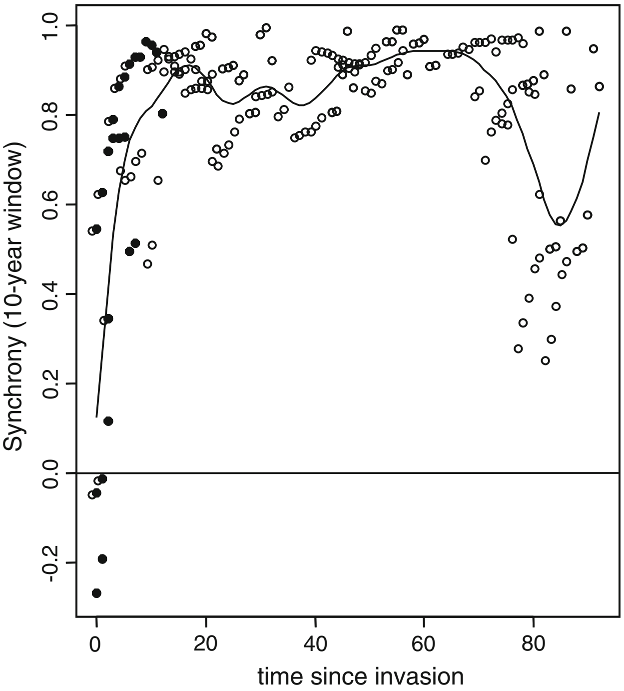

Fig. 4 *Filled circles* the 10-year moving-window correlation between the defoliation time series of each of the post-1975 5-year invasion cohorts with the regional time series for counties invaded prior to 1975 (see Fig. 2). *Open circles* The comparable 10-year moving-window correlation for each 5-year invasion cohort dating between 1900 and 1975. For these, the regional time series is calculated from the pre-1975 cohorts but with the cohort in question omitted. The *solid line* represents the smoothing spline of correlation against time

The initial anti-synchrony of newly established gypsy moth populations may at first glance seem curious. Initial *a*synchrony might be anticipated in newly founded populations because disruptive mechanisms such as demographic stochasticity are likely to play an important role in new and small populations. There is little reason why such stochasticities should lead to anti-synchrony. In the case of the gypsy moth, however, there is a strong Allee effect (Tobin et al. 2007) that only allows invasion pulses to occur when the donor populations surpass a donor threshold density (Johnson et al. 2006b). Nascent populations, therefore, are usually seeded to start growing when the donor populations within the established range are abundant and, as a consequence, about to crash (Johnson et al. 2006b). It remains to be determined whether initial anti-synchrony is prevalent in other invasive species that are influenced by strong Allee effects.

Discussion

Outbreaking forest insects are pests for two reasons. First is their ability to reach "outbreak" densities. This is a property that has received in-depth attention throughout the history of ecology. Second is the geographic synchrony of their population peaks. This spatial synchrony dilutes the regulating effects of natural enemies, reduces the landscape's capacity for ecological buffering, exacerbates the economic burden on individual stakeholders, and overwhelms the budgetary and logistical abilities of agencies. Synchronization of dynamics is therefore a key determinant of the ecological and economic impacts of forest defoliating insects. A principal cause of the difficulty in deducing the causes of synchrony is that most forest insect populations are already synchronized and thus the actual process of synchronization can rarely be observed. We propose that studying synchronization across invasion fronts offers unique opportunities for understanding spatial synchrony.

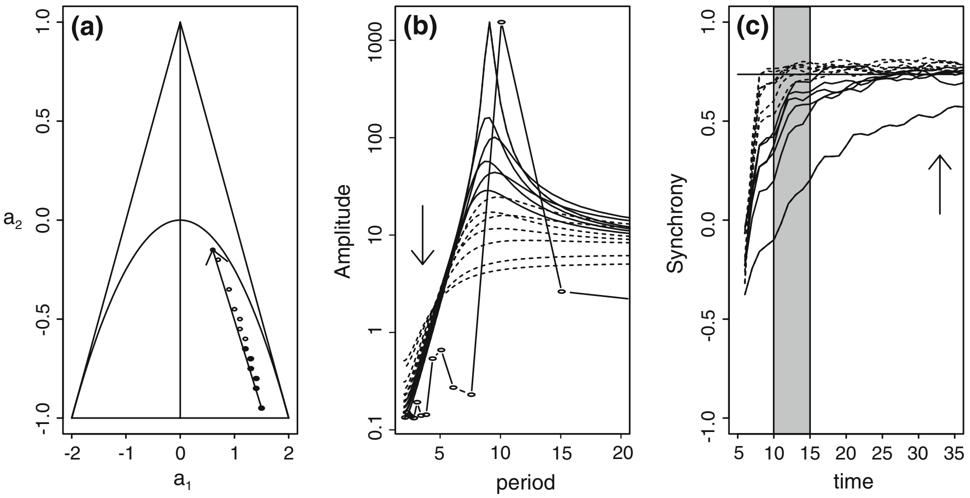

Fig. 5 **a** Sample parameters that correspond to dampening periods with an 8- to 10-year periodicity. *Filled circles* represent parameters for which stochastic dynamics are clearly cyclic, *open circles* represent parameters for which dynamics are only weakly cyclic (see **b**). **b** Theoretical power spectra calculated from Eq. 4. *Solid lines* correspond to parameters for which stochastic dynamics are clearly cyclic (*filled circles* in **a**). *Dashed lines* correspond to parameters for which stochastic dynamics are weakly cyclic (*open circles* in **a**). The *circles* represent the scaled power spectrum of the observed regional defoliation time series (Fig. 3). **c** Correlation as a function of time using a 10-year moving window. The *shaded* region corresponds to the 10- to 15-year time to synchronization seen in the empirical data (see Fig. 4). The *horizontal line* represents the expected asymptotic correlation (ρ) for these simulations. The *arrows* in the figures orient how movements in parameter space (**a**) translate into changes in theoretical power spectra (**b**) and time to synchronization (**c**)

Using Moran's theorem for population synchrony as a starting point, we studied the second-order log-linear (autoregressive) model—as it is commonly used both in the study of population synchrony (e.g., Moran 1953a; Royama 1992) and gypsy moth outbreak dynamics (e.g., Peltonen et al. 2002; Liebhold et al. 2006)—to investigate determinants of the time to synchronization in populations that are coupled by regionalized stochasticity. Generally, we found the time to synchronization to be a function of the overall strength of regulation, the strength of delayed density dependence, and/or the system relaxation time. While the environmental correlation is the crucial determinant of the asymptotic synchrony (cf. Moran's theorem), this parameter did not appear to influence the transient process of time to synchronization, nor did the cycle period. One particularly important finding is that the time to synchronization can be very long for populations that have strong delayed density dependence. This is interesting because strong delayed density dependence is usually important in cyclically outbreaking species. A corollary is that we may expect some invading outbreak pests to be less devastating during the early phase of an invasion. Such effect has previously been suggested to occur because of Allee effects (Johnson et al. 2006b). Here we suggest it may also come about because of slow rates of synchronization during the initial ecological transience.

In the case study of the gypsy moth, the rate of synchronization is very fast. While we have no conclusive explanation for this rapid synchronization, we feel it useful to speculate on the extent to which it is consistent with the standard yardstick in spatial ecology, Moran's theorem. To do this we focus on the part of the parameter space that has a statistical period of 8–10 years (Fig. 5a) and assume 80% correlation in the environment.

Note that while there is a substantial wedge in the parameter space that has a dominant 8- to 10-year period, the strength of the periodicity varies greatly across this region (Fig. 5b). When the delayed density dependence (a_2) is strong and negative, the periodicity is clear. However, while there are $\{a_1, a_2\}$ parameter combinations closer to the origin that have a dominant periodicity in the 8–10 year range, the statistical periodicity is weak. In fact close to the origin there are parameters that give a damping period, T, of 8–10 generations (open circles in Fig. 5a), yet their corresponding power spectra (Eq. 4) do not have a discernible interior mode (dashed lines in Fig. 5b). While autoregressive model fitting of gypsy moth defoliation time series often yields parameter estimates close to the origin (see for example Liebhold et al. 2006), the theoretical power spectra for these parameters are not easily reconciled with observed spectra (Fig. 5b, see also Johnson et al. 2006a).[2]

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[2] This may be a case where the inevitable observation errors in the binary gypsy moth defoliation time series is biasing the autoregressive estimates of direct and delayed density dependence (Dennis and Taper 1994; Solow 1995). More elaborate state-space methods that explicitly model the observational process may be needed to correct for any such bias (e.g., de Valpine 2002; Clark and Bjørnstad 2004).

Figure 5c shows the transient patterns of synchronization for a range of parameters relevant to the gypsy moth 8- to 10-year cycle. As can be seen, synchronization can be very rapid, but only for very weakly periodic populations. In contrast, models that exhibit the degree of periodicity seen in the gypsy moth—a scaled version of the power spectrum of the great attractor time series is superimposed on the AR2 spectra in Fig. 5b—generally take much longer to synchronize, typically as much as 30–40 years but up to 100 years in the most extreme case. Thus, the synchronization seen in the gypsy moth along the invasion front seems to be much faster than predicted from the second-order log-linear model.

We can only speculate on the ecological mechanism that may account for the rapid synchronization in the gypsy moth. Our historical data seem to suggest that there is a very strong penalty for being out of synch. A possible culprit may be the guild of natural enemies. Liebhold and Elkinton (1989) and Gould et al. (1990) attempted to experimentally initiate gypsy moth outbreaks within the established North American range and found that such populations quickly collapsed because of enhanced parasitoid attack rates. Aggregative responses of more-or-less mobile natural enemies may therefore be disproportionately penalizing growth in populations that are out of synch. One additional area to explore in the future is whether the speed of synchronization may be molded by nonlinearities. Previous theoretical studies have shown that nonlinearities can greatly affect the asymptotic synchrony relative to that expected from Moran's theorem (Grenfell et al. 1998; Bjørnstad 2000; Royama 2005). This may be of broad relevance to outbreaking forest insects because many of them exhibit population cycles (Myers 1988; Liebhold et al. 2000; Berryman 2002). While there is often considerable debate about the precise mechanisms responsible for population cycles, there is general consensus that most forest insect cycles result from trophic interactions that often result in nonlinearities in dynamics (Kendall et al. 1999; Dwyer et al. 2004).

Gypsy moth outbreaks within the established range in the USA are highly synchronized. With respect to mechanism, one plausible candidate to explain this is the indirect influence of oak masting—intermittent but geographically synchronized production of acorns by oak trees (Koenig and Knops 2000; Liebhold et al. 2000, 2004b). The small mammals that are important predators of gypsy moth pupae, such as *Peromyscus* (Smith 1981), are strongly influenced by the availability of acorns (Wolf 1996; Elias et al. 2004). Synchronized oak mast will synchronize rodent dynamics and pupal predation, and thereby provide a functional vehicle for the Moran effect on gypsy moth populations mediated by community interaction.

Inferring process from pattern is a challenging task, yet one that has seen a lot of use and a fair degree of success in ecology. One area where this approach is frequently used is in spatial ecology, and particularly with reference to whether the observed spatial synchrony can be accounted for by regionalized environmental stochasticity. The yardstick here is Moran's theorem. However, as recently pointed out by Abbott (2007), this approach is complicated by the fact that similar patterns can result from very different models of how stochasticity affects dynamics. Also, local nonlinearities and local movement can interact to mimic patterns of synchrony predicted by Moran's theorem (Bjørnstad 2000). Moreover, geographical heterogeneities in local dynamics will cloud the theoretically clear-cut relation between synchrony-by-distance and climatic-correlation-by-distance (Peltonen et al. 2002; Hugueny 2006; Liebhold et al. 2006).

Here, we propose that an important way forward for disentangling these complexities is to focus on the transient process of *synchronization* rather than trying to match synchrony-by-distance and climatic-correlation-by-distance within endemic regions. The study of transient dynamics has recently been emphasized as an important way to understand ecological dynamics in general (Hastings 2001), and our study adds to this call. We furthermore advocate that it may be time to treat Moran's theorem as a *null* model against which one should seek to find evidence of departure, rather than the prevailing tradition of treating it as a research hypothesis for which one tries to find support.

Acknowledgments This work was supported by the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service with grants to O.N.B. and A.M.L. (2002, 2006), and D.M.J. (2006).

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