Spatial synchrony propagates through a forest food web via consumer–resource interactions

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Abstract. In many study systems, populations fluctuate synchronously across large regions. Several mechanisms have been advanced to explain this, but their importance in nature is often uncertain. Theoretical studies suggest that spatial synchrony initiated in one species through Moran effects may propagate among trophically linked species, but evidence for this in nature is lacking. By applying the nonparametric spatial correlation function to time series data, we discover that densities of the gypsy moth, the moth's chief predator (the white-footed mouse), and the mouse's winter food source (red oak acorns) fluctuate synchronously over similar distances (~1000 km) and with similar levels of synchrony. In addition, we investigate the importance of consumer–resource interactions in propagating synchrony among species using an empirically informed simulation model of interactions between acorns, the white-footed mouse, the gypsy moth, and a viral pathogen of the gypsy moth. Our results reveal that regional stochasticity acting directly on populations of the mouse, moth, or pathogen likely has little effect on levels of the synchrony displayed by these species. In contrast, synchrony in mast seeding can propagate across trophic levels, thus explaining observed levels of synchrony in both white-footed mouse and gypsy moth populations. This work suggests that the transfer of synchrony among trophically linked species may be a major factor causing interspecific synchrony.

Key words: Erythrobalanus; food web; gypsy moth; indirect effect; Lymantria dispar; *mast seeding; Moran effect; nucleopolyhedrosis virus, NPV;* Peromyscus leucopus; *red oak acorn; regional stochasticity; white-footed mouse.*

INTRODUCTION

In 1953, Patrick Moran proposed that spatially correlated, exogenous effects on population growth can synchronize fluctuations among spatially disjunct populations with similar density-dependent structure (Moran 1953). In the following decades, many empirical and theoretical studies have explored the ability of this process, known as the Moran effect, to explain observations of spatial synchrony in a diversity of study systems (e.g., Grenfell et al. 1998, Bjørnstad et al. 1999, Hudson and Cattadori 1999, Koenig 2002, Peltonen et al. 2002). Moran effects are generally considered to be caused by the direct effects of weather on the survival and reproduction of individual species. Until Cattadori et al.'s (2005) study, there was little consideration of the possibility that exogenous effects may indirectly synchronize a given species by influencing the abundance of

resource or consumer species. Cattadori et al. (2005) found that weather synchronized populations of grouse not by directly affecting the survival or reproduction of the grouse, but indirectly by influencing its interactions with a gastrointestinal parasite. Since this discovery, theoretical studies using two-patch (Ripa and Ranta 2007) or metapopulation models (Abbott 2007) have shown that spatial synchrony of a focal species (due to a Moran effect) may be transferred to a second species via a trophic interaction. Consumer–resource interactions were shown to promote spatial synchrony prior to Cattadori et al.'s (2005) work, but predominantly in the context of a predator that synchronizes prey populations by dispersing among localized prey outbreaks (Ydenberg 1987, Ims and Steen 1990).

For many food webs, the task of determining whether spatial synchrony spreads among species via consumer–resource interactions would be daunting. Spatial synchrony of the constituent species can also be generated by Moran effects acting on each species or by dispersal of individuals between populations (Ims and Steen 1990, Hanski and Woiwod 1993). It is not clear how one would use observational data on population fluctuations

to discern the synchronizing mechanism, and experiments isolating these effects may be impractical (but see Huitu et al. 2005). Furthermore, large-scale spatiotemporal data sets of single species, much less multiple species, are rare. One approach to exploring the consequences of the spread of synchrony among species via consumer–resource interactions would be to combine empirical analysis of patterns of synchrony with mechanistic food web modeling.

The gypsy moth (*Lymantria dispar* L.) and its natural enemies in North America represent an ideal study system to explore interactions between Moran effects and synchronization via consumer–resource interactions. Gypsy moth outbreaks are known to occur with moderate levels of synchrony over several hundred kilometers (Peltonen et al. 2002, Bjørnstad et al. 2008). Largely because of the widespread forest defoliation associated with gypsy moth outbreaks, the natural history and population dynamics of the gypsy moth and its natural enemies have been studied extensively (reviewed in Elkinton and Liebhold 1990). The gypsy moth's population dynamics appear to be strongly influenced by both generalist rodent predators and a viral pathogen (a nucleopolyhedrosis virus, NPV). Moreover, a mechanistic model of interactions between these species generates periodic outbreaks of gypsy moths with behavior similar to that observed in nature (Dwyer et al. 2004).

We used large-scale spatiotemporal data sets to compare patterns of spatial synchrony in the fluctuations of the gypsy moth, the gypsy moth's chief predator (the white-footed mouse, *Peromyscus leucopus* Rafinesque), and the primary winter food source of the white-footed mouse (acorns). In addition, we used a simulation model to evaluate whether synchrony in these species can be explained by Moran effects acting on a single species and synchronization diffusing across the food web via consumer–resource interactions. Our results suggest that synchrony in mast seeding of red oaks caused by regional stochasticity is a major cause of synchrony in white-footed mouse, gypsy moth, and NPV populations.

METHODS

Study system

Gypsy moth population cycles are thought to be driven primarily by their interactions with specialist pathogens such as NPV (Dwyer et al. 2004). The disease caused by NPV has been observed in North America since the early 1900s (Glaser and Chapman 1913, Doane 1970). Virus-induced mortality increases rapidly with increasing gypsy moth density and ultimately terminates gypsy moth outbreaks (Elkinton and Liebhold 1990). Whereas specialist pathogens are implicated in generating gypsy moth cycles, the timing of the onset of outbreaks may be mainly influenced by generalist rodent predators (Elkinton and Liebhold 1990, Elkinton et al. 1996; Bjørnstad et al., *in press*). When gypsy moth

population density is low, predation on pupae by generalist rodents (primarily the white-footed mouse) is the largest source of mortality and principle determinant of gypsy moth population growth. Gypsy moth populations are most likely to increase toward outbreak levels if predator densities are low. In the eastern United States, populations of the white-footed mouse crash approximately every 4–6 years (Wolff 1996, Elias et al. 2004). These mouse population oscillations are attributed, in part, to mast seeding (i.e., synchronous production of large crops of seeds) in oaks; mice are dependent on acorns for overwinter survival (Elkinton et al. 1996, Wolff 1996, Jones et al. 1998, Elias et al. 2004, Clotfelter et al. 2007).

Patterns of synchrony in acorns, mice, and gypsy moths

Time series data derived from several field studies (Table 1, Fig. 1) conducted in eastern deciduous forest were used to explore patterns of spatial synchrony in acorn production, white-footed mouse populations, and gypsy moth populations. Because acorns of the *Erythrobalanus* subgenus (hereafter red oaks) are particularly critical for the winter survival and density of granivorous rodents (Shimada and Saitoh 2006), we used acorn time series in which the acorns were all or predominantly red oak. We used the fraction of forest defoliated within 64×64 km quadrats ($n = 70$) as a proxy for gypsy moth density (Peltonen et al. 2002, Johnson et al. 2006). Levels of defoliation were obtained by analyzing annual aerial defoliation survey maps from the northeastern United States over a period of 31 years (1975–2005). These maps were digitized and represented as sequential raster layers in a geographical information system. Analyses here were restricted to regions designated as part of the 1975 "generally infested area" in USDA gypsy moth quarantine regulations (U.S. Code of Federal Regulations, Title 7, Chapter III, Section 301.45). Data from areas more recently infested by the gypsy moth were not included in our analysis because they have only a short history of defoliation. We also excluded any quadrats in which fewer than three defoliation events were detected. Additional details of the methods used to quantify defoliation levels are found in Liebhold et al. (1997) and Johnson et al. (2006).

We evaluated the manner in which the synchrony in acorns and gypsy moths declined with increasing distance between study locations using the nonparametric correlation function (NCF; Bjørnstad et al. 1999). We obtained confidence intervals for the correlation functions using bootstrap resampling based on 1000 iterations. The number of white-footed mouse time series was too small ($n = 5$) to compute the NCF, hence the synchrony–distance relationship in mice was evaluated using linear regression. Because sampling procedures varied from study to study, correlation functions calculated based on the raw data would likely introduce bias. Therefore, the time series were standardized (after

TABLE 1. Description of time series data sets of red oak (*Erythrobalanus*) acorn, white-footed mouse (*Peromyscus leucopus*), and gypsy moth (*Lymantria dispar*) populations in the United States.

Location	No. locations	Time period	Data source
Red oak acorns			
North Carolina	1	1962–1973	Beck (1977)
Pennsylvania	1	1968–1994	Cogan (1995)
Pennsylvania	1	1974–1986	Drake (1995)
Missouri	1	1981–1988	Sork et al. (1993)
Maryland	1	1986–1996	Healy et al. (1999)
Maine	1	1983–2002	Elias et al. (2004)
Virginia and Maryland	36	1972–2000	Fearer et al. (2008)
White-footed mice			
Vermont	1	1979–1994	Brooks et al. (1998)
Ohio	1	1973–1995	Lewellen and Vessey (1998)
Virginia	1	1979–1993	Wolff (1996)
Pennsylvania	1	1979–1999	Merritt et al. (2001)
Maine	1	1984–2005	Elias et al. (2004)
Gypsy moths			
Northeastern USA	70†	1975–2005	Johnson et al. (2006)

† Number of 64 × 64 km forest quadrats.

log transformation) such that each had a mean of 0 and a standard deviation of 1.

Modeling environmental stochasticity

The effects of environmental stochasticity on the synchrony of acorn production and populations of the white-footed mouse, gypsy moths, and NPV were simulated in a one-dimensional landscape of 300 discrete patches (neighboring patches separated by 5 km). Environmental stochasticity was modeled based on temperature and precipitation observations coincident with the range of the gypsy moth in North America (Peltonen et al. 2002). Temperature and precipitation influence gypsy moth densities (Elkinton and Liebhold 1990) and are considered to be the chief environmental conditions influencing spatial and temporal patterns of mast seeding (Koenig et al. 1999, Koenig and Knops 2000, Kelly and Sork 2002). Because the relative importance of temperature and precipitation to the full suite of species in this system are unknown, the model was parameterized such that the correlation in simulated weather matched the average of the correlations of these two variables. The average of the correlations of temperature and precipitation did not approach 1 for adjacent quadrats (Peltonen et al. 2002). Thus, we modeled total stochastic variation in the population growth rate of species x in patch i in year t, represented by $v_{x,i,t}$, as the mixture $rL_{x,i,t} + (1 - r)R_{x,i,t}$, where $L_{x,i,t}$ and $R_{x,i,t}$ represent local and regional stochasticity, respectively, and r is the relative importance of local vs. regional stochasticity. The variables $L_{x,i,t}$ and $R_{x,i,t}$ are both zero-mean, random normally distributed variables with variance (σ^2) arbitrarily set at 0.1. The ratio of local to regional stochasticity, which is controlled by r, was set at 30%:70% to match the observed level of spatial correlation in weather (Peltonen et al. 2002). The values

representing local ($L_{x,i,t}$) and regional ($R_{x,i,t}$) stochasticity were drawn separately for acorns, mice, gypsy moths, and pathogens because it is not known whether identical weather conditions would have the same or even similar effects on the growth of these populations.

Following Abbott (2007), the regional component of stochasticity in weather acting on species x patch i in year t was modeled as $R_{x,i,t} = E_{x,t}(i)$, where $E_{x,t}(i)$ is the ith element of a multivariate zero-mean, normally distributed random variable with variance–covariance matrix **C**. The covariance in stochasticity acting on patches i and j in year t decreases with distance ($d_{i,j}$) according to the equation $\mathbf{C}(i, j) = \sigma^2 \exp(-gd_{i,j})$, where g is a constant that controls the rate at which the covariance decays with distance. We approximated observed levels of synchrony in actual weather data (June mean temperature and June precipitation; Peltonen et al. 2002) from the gypsy moth's range by setting the covariance decay parameter, g, to 0.00125. This resulted in a close match between the nonparametric correlation functions estimated from simulated stochasticity (e^v) and the mean of the nonparametric correlation functions for temperature and precipitation.

To mimic the periodic nature of fluctuations in the production of red oak acorns (Appendix A), acorn dynamics were modeled using a spatially extended stochastic second-order log-linear model (Royama 1992):

$$X_{i,t} = \beta_0 + (1 + \beta_1)X_{i,t-1} + \beta_2 X_{i,t-2} + v_{x,i,t}. \quad (1)$$

The variable $X_{i,t} = \log(A_{i,t})$, where $A_{i,t}$ is the abundance of acorns at patch i in year t. The intercept term, β_0, was set to 3.3 because the resulting periodicity of gypsy moth populations in model simulations closely matched the periodicity of natural populations. The parameters β_1 and β_2 represent the strength of density dependence at
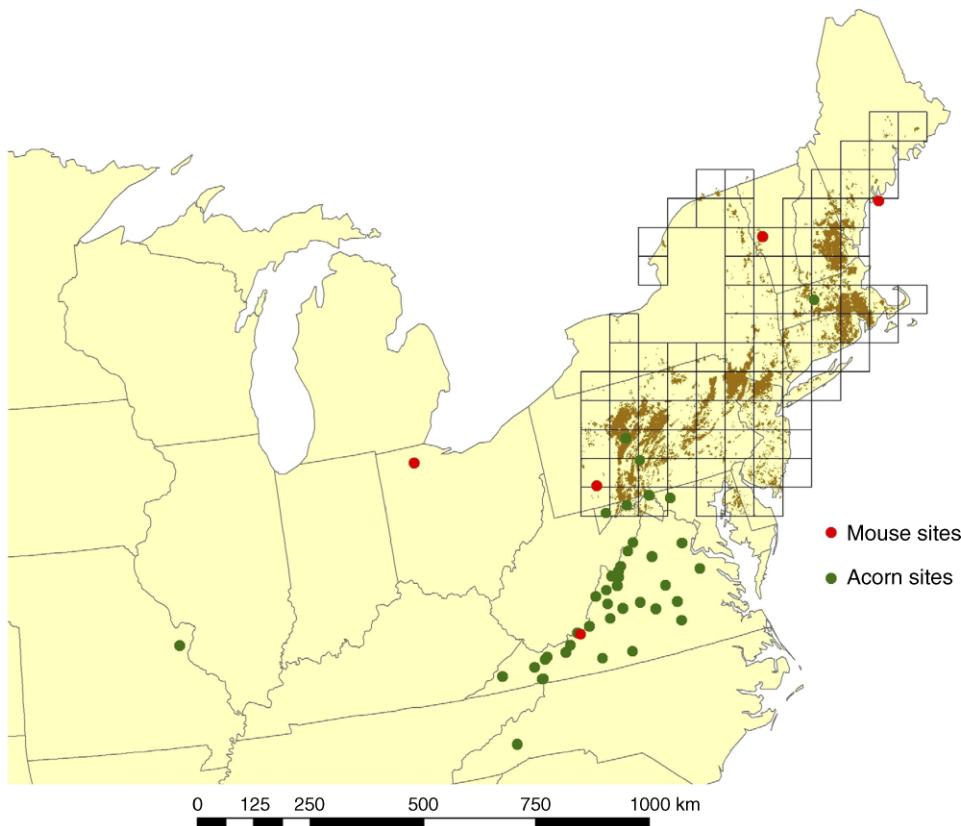
Fig. 1. Source locations of red oak acorn (*Erythrobalanus*), white-footed mouse (*Peromyscus leucopus*), and gypsy moth (*Lymantria dispar*) abundance data sets. For each forest quadrat (black outlined squares), the percentage of forest canopy defoliated was used as a proxy of gypsy moth abundance in a given year. Areas defoliated by gypsy moths between 1975 and 2005 are marked in brown.

time lags of one and two years, respectively. To mimic the magnitude and five-year period of fluctuations in acorn abundance we set β_1 and β_2 at 0.6 and −0.9, respectively.

Because numerical responses of generalist mammal predators to increases in gypsy moth abundance are highly constrained (Elkinton and Liebhold 1990), we assumed that gypsy moth abundance had no effect on the population growth of the mice. Based on statistical analysis of a 13-year data set on acorn and white-footed mouse density (Wolff 1996), Schauber (2001) found that the density of white-footed mice was most parsimoniously modeled as a linear function of acorn density (see also Clotfelter et al. 2007). More complex models with density-dependent effects on mouse population growth provided only slightly better fits than the simple linear regression model. Thus, we modeled mouse density ($M_{i,t}$) as

$$M_{i,t} = (q + mA_{i,t-1})\exp(v_{x,i,t}). \qquad (2)$$

We used Schauber's (2001) empirical estimate for the regression coefficient ($m = 0.6$). However, because we found that model runs using the empirical estimate of the intercept (7.28) resulted in predator densities so high

that the gypsy moth did not exhibit outbreaks, we set $q = 0$. The r^2 values of the relationship between acorn density and mouse density produced from trial runs of the model ($r^2 = 0.84 \pm 0.02$ [mean $\pm$ SE], $n = 10$) corresponded closely with Schauber's (2001) empirical estimate of $r^2 = 0.79$.

To model interactions between gypsy moths, white-footed mice, and NPV, we spatially extended a model developed by Dwyer et al. (2004). The fraction of larval gypsy moths infected by NPV, $I(N_{i,t}, Z_{i,t})$, varies with larval and pathogen density in patch i in year t ($N_{i,t}$ and $Z_{i,t}$, respectively) according to

$$1 - I(N_{i,t}, Z_{i,t}) = \left\{ 1 + \frac{1}{k} \left[N_{i,t}I(N_{i,t}, Z_{i,t}) + Z_{i,t} \right] \right\}^{-k} \qquad (3)$$

where k is the inverse squared coefficient of variation of the transmission rate (Dwyer et al. 2004). The density of larvae surviving to the pupal stage in patch in year t is then

$$N'_{i,t} = \lambda N_{i,t}\left[1 - I(N_{i,t}, Z_{i,t}) \right] \qquad (4)$$

where λ is the gypsy moth's finite rate of increase. The density of pathogens in patch i in year $t + 1$ is given by
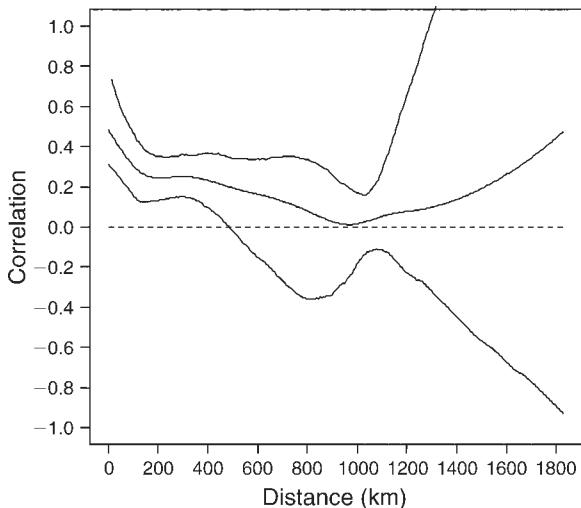
FIG. 2. The spatial correlation function of red oak acorn density data. The upper and lower lines represent 95% bootstrap confidence intervals.

$Z_{i,t+1} = \phi N_{i,t} I(N_{i,t}, Z_{i,t})$, where ϕ is the between-season growth rate of the pathogen (Dwyer et al. 2004). Accounting for local and regional stochasticity, the full model of virus dynamics is then

$$Z_{i,t+1} = \phi N_{i,t} I(N_{i,t}, Z_{i,t}) \exp(v_{x,i,t}). \qquad (5)$$

To model predation of gypsy moth pupae by white-footed mice we use a type II functional response (Elkinton et al. 2004, Schauber et al. 2004) instead of the type III functional response assumed by Dwyer et al. (2004). The instantaneous rate of predation for the type II model is given by $M_{i,t} ac/(c + N'_{i,t})$ and the per capita probability of escaping predation is $\exp(-M_{i,t} ac\Delta t/(c + N'_{i,t}))$, where $N'_{i,t}$ is given in Eq. 4 (Bjørnstad et al., *in press*). Here, Δt is the duration of the pupal stage (~ 10 d), and a and c are constants determining the predator's maximum attack rate and half-saturation point. The functional response for which the maximum predation rate ($= 1 - \exp(-aM/2)$) and the half saturation point occur at the same prey densities that they do in Dwyer et al.'s (2004) type III functional response, but having type II form is given by $ab(2 + \sqrt{3})M_{i,t}/2[N'_{i,t} + b(2 + \sqrt{3})]$, where $c = b(2 + \sqrt{3})$ (Bjørnstad et al., *in press*). Our model of adult gypsy moth dynamics (including local and regional stochasticity) is then

$$N_{i,t+1} = N'_{i,t} \exp\left\{ -\frac{ab(2 + \sqrt{3})M_{i,t}}{2\left[N'_{i,t} + b(2 + \sqrt{3})\right]} \right\} \exp(v_{x,i,t}). \quad (6)$$

We used values for the parameters in Eqs. 3–6 that are similar to estimates derived from field experiments (Elkinton et al. 1996, Dwyer et al. 2004; $k = 1.06$, $a = 0.98$, $b = 0.05$, $\lambda = 74.6$, and $\phi = 21.33$). To prevent extinctions of populations and to mimic the magnitude of density fluctuations observed in gypsy moth popula-

tions in nature, we set minimum allowable densities of 0.1 and 0.0001 for gypsy moths and NPV, respectively.

Due to the limited mobility of gypsy moths (females are flightless in North American populations) and mice, dispersal of these species is not likely to explain observations of synchrony in gypsy moths over broad geographic areas (Peltonen et al. 2002). In addition, although the rate of spread of NPV appears to exceed that of ballooning gypsy moth larvae (Dwyer and Elkinton 1995), pilot modeling studies indicated that dispersal of NPV did not have a synchronizing effect on gypsy moth populations (K. J. Haynes, *unpublished data*). Therefore, dispersal was not included in our model.

Initial densities for each species were drawn from random normal distributions, and the model was run for 150 generations. To reduce the influence of transient dynamics resulting from initial conditions, the first 50 years of data from each time series were discarded prior to statistical analysis of the time series. Then, to evaluate the impacts of the spread of Moran-effect-induced synchrony through ecological interactions, we systematically removed the effects of regional stochasticity from one species at a time by setting the relative importance of regional stochasticity $(1 - r)$ to zero and the relative importance of local stochasticity to 1. For each replicate simulation of the model, we evaluated how synchrony in each species declined with increasing distance between patches using the nonparametric correlation function (Bjørnstad et al. 1999).

RESULTS

Spatial synchrony in acorn, mouse, and gypsy moth data

Spatial synchrony generally decreased with increasing lag distance at each trophic level (Figs. 2–4). Whereas spatial synchrony of the white-footed mouse appeared to decline linearly with increasing lag distance (correlation $= -0.0007 \times$ distance (km) $+ 0.62$, $P = 0.006$, $n = 10$, $r^2 = 0.64$), the rapid declines in the synchrony of the acorn and gypsy moth data at short distances were followed by slowly declining or steady levels of synchrony (Figs. 2 and 4). Synchrony appeared to increase with increasing lag distance in the acorn data at lag distances >1000 km, but there was substantial uncertainty at these long lag distances (Fig. 2). The lag distances at which the spatiotemporal correlation declined to 0 did not differ strongly among species. For both acorns and the mouse, the correlation declined to 0 at lag distances of ~ 1000 km (Figs. 2–3), though for the acorns the correlation was not significantly different from 0 for lag distances >500 km (Fig. 2). Spatiotemporal correlations in the gypsy moth data were >0 over the full range of observed lag distances 0–960 km and significantly greater than 0 up to a lag distance of ~ 900 km (Fig. 4).

Levels of synchrony in the acorn and mouse data were very similar for lag distances <1000 km. The gypsy moth showed higher levels of synchrony than both acorns and the white-footed mouse; however, the
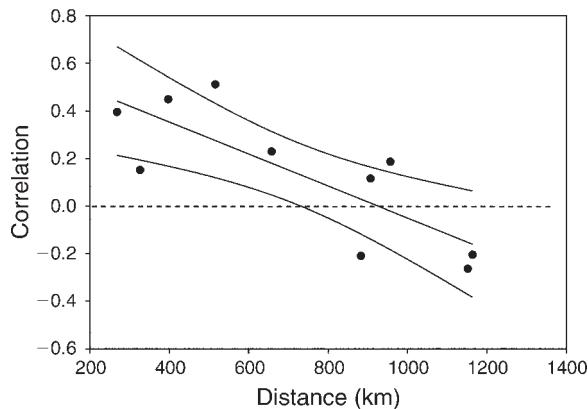
FIG. 3. Relationship between population synchrony (correlation) and distance estimated from white-footed mouse data. The upper and lower lines represent 95% confidence intervals.

confidence intervals for all three correlation functions overlapped extensively.

Spatial synchrony in simulated populations

The model predicted that when all species were affected by regional stochasticity, all species were partially synchronized and synchrony declined with distance (Fig. 5A). The correlation functions of each species paralleled that of simulated weather, in that the correlations decreased most rapidly at short distances (Fig. 6). Levels of synchrony were higher for acorns and mice than for gypsy moths and NPV.

For simulated mammal and gypsy moth populations, indirect synchronization via trophic interactions was stronger than direct impacts of regional stochasticity. As would be expected from the structure of the model, removal of regional stochasticity completely eliminated synchrony in acorn production (Fig. 5B). In contrast, the mean correlation in mouse density at a lag distance of 200 km dropped only slightly, from 0.6 to 0.5, upon removing regional stochasticity in mouse population growth (Fig. 5C). At long lag distances (>600 km), the gypsy moth actually displayed higher synchrony in the absence of regional stochasticity than in its presence (Fig. 5D). Finally, the level of synchrony in NPV was unaffected by direct regional stochasticity (Fig. 5E).

When the effect of regional stochasticity on acorn production was removed, not only did synchrony in acorns disappear, but there were also sharp drops in the synchrony of mice, gypsy moths, and NPV. Regional stochasticity effects on acorn production had clear effects on correlations in mouse, gypsy moth, and NPV populations up to lag distances of 900–1200 km.

Removal of regional stochasticity effects on the white-footed mouse also resulted in lower levels of synchrony in gypsy moths and NPV. However, these indirect effects were weaker than those caused by removal of regional stochasticity on acorn production. For example, the distance over which gypsy moth populations exhibited

synchrony decreased by ~600 km when effects of regional stochasticity were removed from acorn production, but only decreased by 300 km when regional stochasticity effects were removed from mouse populations. Based on a sensitivity analysis, these results were consistent over a wide range of parameter values (Appendix B).

DISCUSSION

We show that red oak acorns, white-footed mice, and gypsy moths exhibit similar patterns of spatial synchrony in eastern deciduous forests of the United States. Spatiotemporal correlations in abundance clearly decline with distance and are generally >0 for lag distances up to 1000 km. Potential explanations for this similarity include a common response of each species to correlated weather conditions (i.e., Moran effects), synchronization of one or more of the species by regional stochasticity resulting in synchronization of the remaining species through trophic interactions (Cattadori et al. 2005, Abbott 2007, Ripa and Ranta 2007), or dispersal of one of the species that then synchronizes the fluctuations of the remaining species (Ydenberg 1987, Ims and Steen 1990). Because of limited dispersal ability of all three populations, the third hypothesis is unlikely to explain observations that synchrony occurs over broad spatial scales in our study system (Peltonen et al. 2002). Furthermore, pilot modeling studies showed that dispersal of mice, gypsy moths, or viruses had little or no effect on levels of synchrony in simulated gypsy moth or virus populations, particularly in the absence of regional stochasticity. This was true across a wide range of realistic rates of dispersal (K. J. Haynes, *unpublished data*).

Considerable research on the dynamics of mast seeding in oaks, mostly from western North America, has demonstrated the existence of both periodicity and
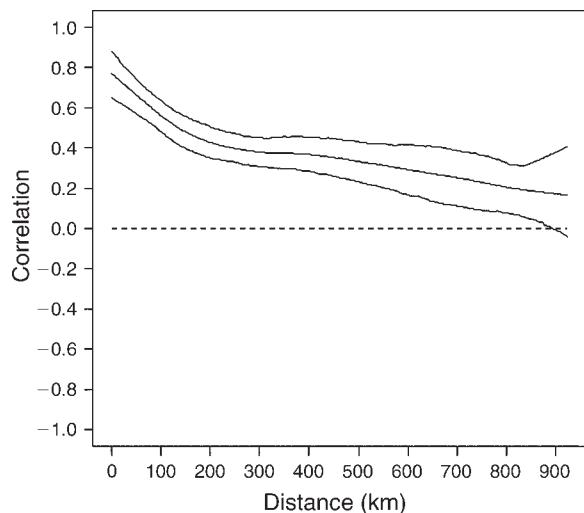

FIG. 4. The spatial correlation function from gypsy moth defoliation data. The upper and lower lines represent 95% bootstrap confidence intervals.
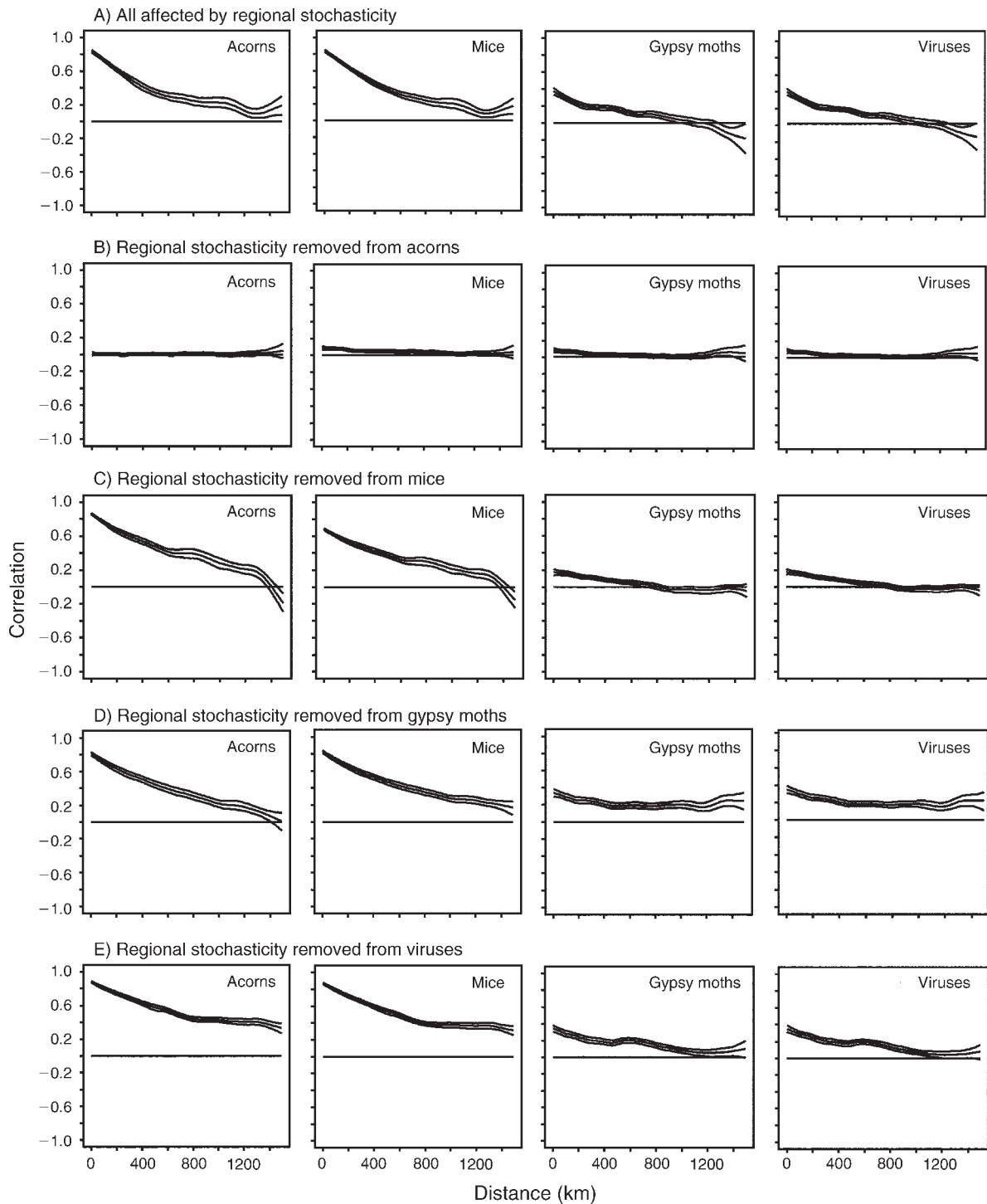
FIG. 5. The spatial correlation functions estimated from models with (A) regional stochasticity affecting each species, (B) no regional stochasticity affecting acorns, (C) no regional stochasticity affecting white-footed mice, (D) no regional stochasticity affecting gypsy moths, and (E) no regional stochasticity affecting the pathogen. The upper and lower lines represent 95% bootstrap confidence intervals.

spatial synchrony in oak mast seeding (Koenig et al. 1999, Koenig and Knops 2000, Kelly and Sork 2002). Many of these same studies have identified regional stochasticity as the cause of synchrony in mast seeding. There also is considerable evidence that resource pulses created by mast seeding have profound effects on a variety of organisms inhabiting oak-dominated forests. Organisms whose population levels are known to track oak mast production include populations of seed-eating rodents, deer, and birds (Wolff 1996, McShea 2000, Elias et al. 2004, Clotfelter et al. 2007, Schmidt and Ostfeld 2007). In addition to the direct effects of mast seeding on the dynamics of consumer populations, additional information indicates that mast seeding indirectly influences the dynamics of populations tro-phically linked to mast consumers. For example, white-footed mice numerically respond to fluctuations in mast abundance; consequently mast dynamics indirectly affect populations of gypsy moths (prey of *Peromyscus*) and ticks (parasites of *Peromyscus*) (Elkinton et al. 1996, Ostfeld et al. 1996, Jones et al. 1998). Though the importance of mast seeding on consumer dynamics has been well documented, there has been little previous investigation of mast seeding effects on synchrony of consumer populations.

Our simulations suggest that synchrony in mast seeding of red oaks caused by regional stochasticity is an important cause of synchrony in the white-footed mouse, gypsy moth, and even NPV populations. When the regional stochasticity acting on acorns was removed, spatial synchrony in the remaining species all but disappeared regardless of whether they themselves experienced regional stochasticity. The presence or absence of regional stochasticity directly affecting gypsy moths or NPV had little influence on levels of synchrony in these species. Though removal of regional stochas-ticity affecting white-footed mouse populations reduced synchrony of mouse, gypsy moth, and NPV popula-tions, this effect was less pronounced than the effect of regional stochasticity on acorn production. Thus, we show that indirect effects of regional stochasticity acting directly on acorn production are a major factor underlying the spatial synchrony of these trophically linked species. Evidence of synchronous food crops promoting synchrony in small mammals is present in other study systems (Korpimaki et al. 2005, Bowman et al. 2008). However, this is the first study to provide both empirical and theoretical evidence that synchrony initiated by regional stochasticity may be disseminated widely throughout a food web, ultimately affecting species occupying a diversity of roles (e.g., herbivores, predators, pathogens).

For a given species, the extent to which population fluctuations are synchronized by regional stochasticity is known to depend on the nature of that species' density-dependent dynamics. Whereas the spatial synchrony of populations whose growth is governed by linear dynam-ics should exactly match the synchrony of environmental
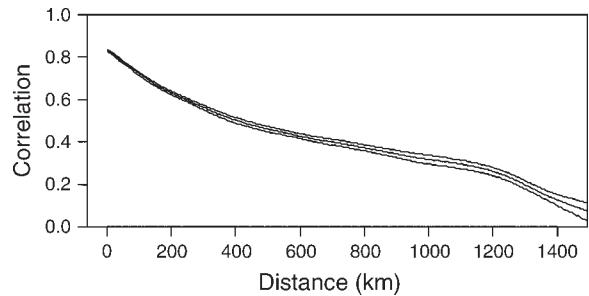

FIG. 6. The spatial correlation function estimated from simulated weather conditions. The upper and lower lines represent 95% bootstrap confidence intervals. The correlation function of the simulated weather conditions closely matches that of temperature and precipitation data for the gypsy moth's range in North America (see Peltonen et al. 2002: Fig. 2).

conditions (Moran 1953), the synchrony of populations governed by nonlinear dynamics may be greater or lower than the correlation of environmental conditions (Gren-fell et al. 1998, Ranta et al. 1998, Bjørnstad 2000). The complexities of nonlinear population growth may explain why simulated gypsy moth and NPV populations could not be synchronized by direct regional stochas-ticity. However, this cannot explain why regional stochasticity had only moderate effects on the synchrony of white-footed mouse populations. Mouse density was modeled as a linear function of acorn density, which was itself produced by a linear autoregressive model. However, because mouse population growth was also affected by acorn production, as in nature (Schauber 2001, Elias et al. 2004), synchrony in the simulated mouse population was less dependent upon regional stochasticity than on a synchronous acorn crop.

Because synchrony in the fluctuations of NPV was minimally increased by the direct effects of regional stochasticity, the gypsy moth could not have been synchronized through the host–pathogen interaction. Simulated populations of the white-footed mouse were synchronized via their interaction with synchronous acorn crops, and this set the stage for the synchrony in mouse populations to be transferred to gypsy moths and, in turn, NPV. In our simulations, gypsy moth populations only escaped from low density and began to outbreak during certain "windows of opportunity" in which mouse densities were low, a finding consistent with empirical data (Elkinton et al. 1996, Liebhold et al. 2000). Predation by rodents is known to be a major factor influencing the growth of low-density gypsy moth populations, and it is thought that sufficiently dense populations of rodents are capable of preventing gypsy moth outbreaks (Elkinton and Liebhold 1990, Liebhold et al. 2000). Furthermore, the hypothesis that a poor acorn crop can lead to low mouse density and, in turn, increase the likelihood of a gypsy moth outbreak was supported by Liebhold et al.'s (2000) study showing a significant lagged correlation between acorn density and forest defoliation.

For a given lag distance, spatial synchrony in the empirical data was generally stronger in the gypsy moth and white-footed mouse than in acorns. In the simulated data, on the other hand, the gypsy moth displayed lower levels of synchrony than the mouse or acorns. This discrepancy may have arisen due to differences in the spatial extent of the sample units between the data sets. Gypsy moth defoliation was measured in 64 km^2 quadrats, whereas acorn and mouse densities were measured in much smaller plots. Using large quadrats can mask spatial variation occurring at smaller spatial scales, thus increasing spatial autocorrelation among sample units (Bellehumeur et al. 1997, Dungan et al. 2002). Alternatively, the discrepancy in levels of synchrony among species could be explained by the manner in which we modeled the effects of regional stochasticity on each component of the food web. We assumed that each species was equally affected by weather. However, it is possible that the gypsy moth is particularly susceptible to weather-driven changes in population growth rate, which would likely increase the synchronizing effect of regional stochasticity. In addition, because it is not known whether identical weather conditions would have similar effects on the population growth of each species, the values representing local and regional stochasticity were drawn separately for acorns, mice, gypsy moths, and pathogens. If, in fact, weather events have correlated effects on different species in this food web, impacts of weather on population growth and synchrony may be compounded across a food web. The direct effects of weather on the population growth and synchrony of a given species may be reinforced by correlated, weather-driven effects on consumer or resource species. Evaluation of this hypothesis will require future theoretical investigation.

Recent theoretical models have been pivotal in demonstrating the potential for regional stochasticity to indirectly influence spatial synchrony among species embedded within food webs (Abbott 2007, Ripa and Ranta 2007). In this vein, our study is the first to use an empirically informed mechanistic model to show that Moran effects and subsequent diffusion of synchrony to other species via consumer–resource interactions may be the primary mechanisms underlying patterns of spatial synchrony observed in a real study system. How commonly synchrony diffuses through consumer–resource interactions in other food webs is an open question. Given that interspecific synchrony has been observed in several different taxa (e.g., birds, small mammals, insects; Koenig 2001, Raimondo et al. 2004, Huitu et al. 2005, Korpimaki et al. 2005), further exploration of the diffusion of synchrony through food webs represents a promising avenue of research.

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APPENDIX A

Results from wavelet analysis of acorn abundance time series data (*Ecological Archives* E090-213-A1).

APPENDIX B

Sensitivity of simulation model results to parameter values (*Ecological Archives* E090-213-A2).