



Spatio-temporal dynamics of a tree-killing beetle and its predator

Aaron S. Weed, Matthew P. Ayres, Andrew M. Liebhold and Ronald F. Billings

A. S. Weed (aaron_weed@nps.gov), National Park Service, 120 Chatham Lane, Fredericksburg, VA 22405, USA. – M. P. Ayres and ASW, Dept of Biological Sciences, Dartmouth College, Hanover, NH, USA. – A. M. Liebhold, USDA Forest Service, Northern Research Station, 180 Canfield St., Morgantown, WV 26505, USA. – R. F. Billings, Texas A&M Forest Service, 200 Technology Way, Suite 1281, College Station, TX 77845, USA.

Resolving linkages between local-scale processes and regional-scale patterns in abundance of interacting species is important for understanding long-term population stability across spatial scales. Landscape patterning in consumer population dynamics may be largely the result of interactions between consumers and their predators, or driven by spatial variation in basal resources. Empirical testing of these alternatives has been limited by the lack of suitable data. In this study, we analyzed an extensive network of spatially replicated time series to characterize the local and regional processes affecting spatio-temporal dynamics of a tree-killing bark beetle (*Dendroctonus frontalis* or SPB) and its key predator (*Thanosimus dubius*) across the southeastern United States. We first used a mechanistic model to evaluate factors affecting the stability of 95 predator–prey time series and then conducted spatial analyses to evaluate scale dependence in the factors affecting the geographical patterning of this system. Across the region, population fluctuations of both species were correlated in space beyond 400 km but there was notable spatial variation in the deterministic and stochastic processes influencing forest-scale (local) fluctuations. Time series analyses indicated that local dynamics of SPB and *T. dubius* are not cyclical. Instead, the abundance of *T. dubius* responded almost instantaneously to changes in SPB abundance. Spatial variation in long-term forest-scale abundance of both species was linked most strongly to the abundance of pine habitat indicating a stronger role for resource availability in SPB population dynamics than top-down effects. Our results are consistent with other studies indicating that animal populations tend to be synchronized in space via spatially correlated processes such as weather; yet local dynamics tend to be linked to smaller-scale host patterns. Our study provides a rare empirical assessment of how local processes scale up to produce landscape patterns that influence forest ecology and forest management.

Resolving the processes that generate spatio-temporal patterns in ecological systems is critical to understanding a wide variety of ecological processes, for example, our understanding of how the spatial organization of populations affects their long term persistence from local to regional scales (Bjørnstad et al. 1999, Borcard et al. 2004). One key theme emerging is that within a single species, population fluctuations are commonly synchronized over large distances ('spatial synchrony'; Bjørnstad et al. 1999, Liebhold et al. 2004), yet the local dynamics and the processes that generate them (e.g. interactions with natural enemies) often vary among geographically disjunct populations (Post 2005, Johnson et al. 2006, Grøtan et al. 2009, Choi et al. 2011). This variation in turn greatly influences the distance at which populations are synchronized in space (Royama 2005) and the resulting long-term spatial pattern (Turchin et al. 1997, Bjørnstad et al. 1999). However, despite recognition that variation in local processes is common, studies are rarely able to isolate and measure the importance of factors affecting long-term local stability at large landscape scales (Cronin and Reeve 2005).

Spatial variation in temporal behavior of population fluctuations is often attributed to gradients in the composition

of natural enemies (Bjørnstad et al. 1995, 2010, Hanski et al. 2001), abiotic conditions (Post 2005), patch quality (Kruess 2003, Thies et al. 2003, Riolo et al. 2015), limits or barriers to dispersal (Turchin et al. 1997), and habitat fragmentation or composition (Roland and Taylor 1997, Bellamy et al. 2003, Haynes et al. 2007). Spatial variation in the composition of natural enemies or their response to habitat quality and structure have been hypothesized to explain spatially variable periodicity in the dynamics of moths and microtine rodents (Bjørnstad et al. 1995, Roland et al. 1998, Klemola et al. 2006, Bjørnstad et al. 2010). However, there is a paucity of empirical evidence at the landscape level documenting spatial variation in the population dynamics of interacting species (Winder et al. 2001, Cronin and Reeve 2005) and consequently our understanding is largely limited to theoretical studies (Hassell et al. 1991, Turchin et al. 1997, Bjørnstad et al. 2002, 2010, Li and Jin 2011).

Understanding how interactions between host and natural enemy populations vary geographically has broad implications for applied pest management. Natural enemies play key roles in regulating pest populations below damaging levels, so understanding how local and regional processes

affect their spatial and temporal responses to host density is important for identifying manipulative tactics to prevent pest damage. For example, agricultural studies indicate that landscape structure, often beyond crop margins, influences pest and natural enemy spatial dynamics (Tscharnke et al. 2005, Gardiner et al. 2009). Further, habitat effects on natural enemy composition, activity, and host use can also influence the dynamics and spatial patterning of outbreaking forest pests (Volney and McCullough 1994, Klemola et al. 2006, Haynes et al. 2012, Nixon and Roland 2012). Bark beetles, especially some members of the genus *Dendroctonus*, are an important group of forest pests that have affected millions of hectares of North American forests in recent years (Meddens et al. 2012). One such species, the southern pine beetle (SPB), *D. frontalis*, has caused major economic losses to the pulp and timber industry in the southeastern USA (Royama 2005) and is now colonizing forests located > 200 km north of this historical range as a consequence of winter warming, threatening most pine forests on the eastern seaboard (Ungerer et al. 1999, Tr an et al. 2007).

Several early studies indicated that SPB exhibited cyclical dynamics in Texas (Turchin et al. 1991, 1999, Reeve and Turchin 2002), and there was evidence that these oscillations were due to the coupled predator–prey dynamics between SPB and *Thanasimus dubius* – adults and larvae of the latter being a voracious predator of SPB adults and larvae (Reeve 1997). However, the signal of cyclical behavior disappeared from the same time series of abundances in east Texas with the addition of another 20 yr of data (Friedenberg et al. 2008). Recent analyses of SPB dynamics across the southeastern U.S. indicated that the large population fluctuations characteristic of SPB are the result of alternate attractors in the demographic feedback system (Martinson et al. 2013) rather than true population cycles (Reeve and Turchin 2002). Alternate attractors produce dynamics in which abundance tends to be either low or high, but without the regularity of fluctuations when populations are governed by cyclical dynamics (Berryman 2002). Thus the population dynamics of SPB appear to be fundamentally different from the cyclical behavior that characterizes most of the Lepidoptera, microtine rodents, and hares that have been previously analyzed for spatial patterns (Ranta et al. 1997, Lambin 1998, Bj ornstad et al. 2002, Peltonen et al. 2002, Klemola et al. 2006). How the underlying processes and the magnitude of their effects affect local to regional scale SPB dynamics might be different from cyclical species ( okland et al. 2005). Knowledge of the factors affecting SPB and its interaction with *T. dubius* at different spatial scales is relevant when assessing outbreak risk of forest stands to SPB across the region (Billings and Upton 2010).

In this study, we used spatially replicated time series of SPB and *T. dubius* abundance monitored across an expansive network in the southeastern USA to characterize the local and regional processes affecting predator–prey dynamics. Our overall goals were to evaluate the factors affecting local stability using a mechanistic model and estimate the spatial synchrony of this predator–prey system. We then tested hypotheses to explain geographical patterning in the predator–prey dynamics at the landscape-scale.

Methods

Study system

SPB is a tree-killing bark beetle with a broad geographic range that extends across the southeastern US and south to Nicaragua (Thatcher 1980). SPB develops on many *Pinus* species across its distributional range, but loblolly *Pinus taeda* and shortleaf pines *P. echinata* are the most susceptible in the southeastern USA (Thatcher 1980, Ylioja et al. 2005, Friedenberg et al. 2007b, Martinson et al. 2007). Beetles mass attack trees (> 12 cm DBH; Lih and Stephen 1996) using a highly effective pheromone communication system to overcome host defenses. Once the host defense is depleted, beetles that successfully survive the host defense burrow through the bark, mate, and females construct egg galleries within the host phloem, which they then inoculate with symbiotic fungi (Hofstetter et al. 2006). Larvae develop on subcortical tissues through four instars and enter the outer bark for pupation. Beetles complete multiple generations per year and the number of generations depends on location and annual temperature patterns (Thatcher 1980, Ungerer et al. 1999). In warmer regions attacking adults are active year-round with more or less overlapping generations (Friedenberg et al. 2007a).

Trees that are being mass-attacked by SPB are simultaneously colonized by the predator *T. dubius*, which is highly attracted to frontalin, the main pheromone component of SPB (Vit e and Williamson 1970, Payne et al. 1984, Erbilgin and Raffa 2001). Adults of *T. dubius* attack SPB adults as they land and attempt to bore into trees. Larvae of *T. dubius* hatch from eggs laid on the bark surface and then enter bark beetle galleries to consume brood. *Thanasimus dubius* shows a strong numerical response to SPB density and can cause considerable generational mortality to SPB (Reeve 1997, Turchin et al. 1999, Reeve and Turchin 2002). It has been hypothesized that mortality by *T. dubius* could be strong enough to stop outbreaks (Reeve 2011).

Study area and SPB and *T. dubius* abundance data

The Texas A&M Forest Service in cooperation with local, state, and federal government agencies have coordinated a spatially extensive network of SPB pheromone trapping sites (frequently located at USDA Forest Service Ranger district offices) since 1986 across the southeastern USA (Fig. 1). The standardized sampling protocol employs funnel traps that are baited with frontalin and α -pinene and monitored for 8 weeks beginning about the time when dogwood (*Cornus*) trees are flowering (Billings and Upton 2010). Traps are situated in the forest understory (usually within patches of hardwoods that are within 50 m of suitable host trees). Captures of SPB and its predator *T. dubius* are counted for the purpose of estimating outbreak risk across the region. At the time of trapping, both SPB and *T. dubius* tend to be dispersed and captures are similar at replicate traps within the same forest; Martinson et al. (2013) reported that 78% of the variation in SPB trap captures was among forests and years, with only the remainder attributable to variation among traps within

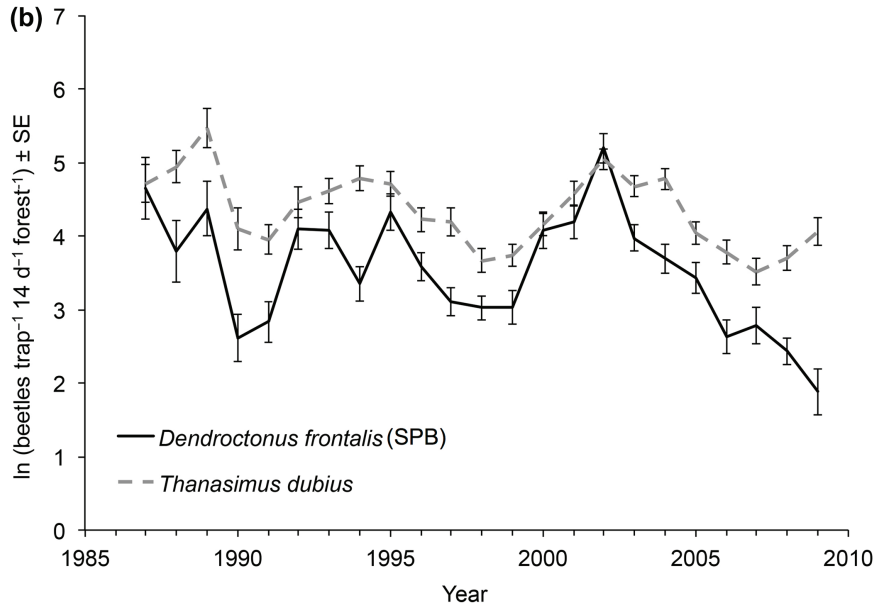
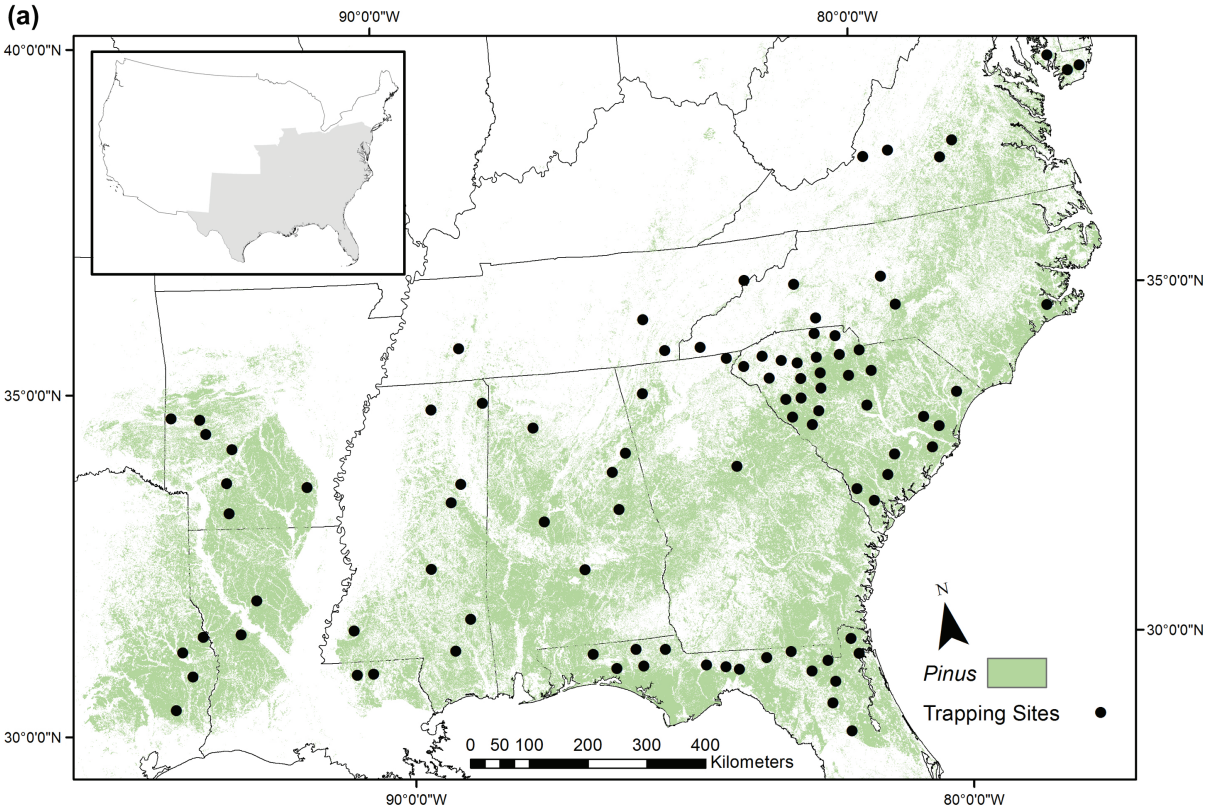


Figure 1. Pheromone traps locations (a) and average population fluctuations (b) of *Dendroctonus frontalis* (SPB) and *Thanasimus dubius* across the southeastern USA.

forests (see also Friedenberget al. 2007b). In this study we analyzed spring trapping data from 95 forests where SPB and *T. dubius* populations had been monitored for 16 ± 4 yr (mean \pm SD) (range: 10 to 23) (Fig. 1). Prior to analyses, each time series was checked for stationarity (by examining autocorrelation functions) and detrended using linear models when necessary. Annual per capita growth

rates (R_t) were calculated for each of the stationary time series using the expressions:

$R_t^N = \ln(N_{t+1} + 1) - \ln(N_t + 1)$ and $R_t^P = \ln(P_{t+1} + 1) - \ln(P_t + 1)$ where N_{t+1} and N_t and P_{t+1} and P_t represent the abundances of SPB and *T. dubius* (beetles trap⁻¹ 14 d⁻¹) within the current (t) and following year ($t + 1$), respectively.

Geographical variation in temporal dynamics

Auto- and cross-correlation of forest-scale time series

We fit autocorrelation functions (ACF) to each of the ln-transformed time series of *D. frontalis* and *T. dubius* abundance to estimate the correlation in abundances to lag(10) for both species in each forest. We then calculated cross-correlation functions (CCF) up to lag(10) between SPB and *T. dubius* time series in each forest to measure temporal synchrony in their dynamics. Average ACF and CCF values were used to assess the spatial variation in the temporal dynamics of SPB and *T. dubius* at the forest-scale. All ACFs and CCFs were fit using R software (ver. 3.1.2).

Statistical models describing temporal dynamics within each forest

A discrete form of a predator–prey model (Eq. 1 and 2) was used as the baseline for evaluating and comparing alternative models to describe the temporal behavior in the per capita growth rates of SPB (R_t^N) and *T. dubius* (R_t^P) within each forest (Royama 1992, Berryman 2003):

$$R_t^N = f(\ln(N_t), \ln(N_{t-1}), \ln(P_t), \ln(P_{t-1})) + \varepsilon_t \quad (1)$$

$$R_t^P = f(\ln(N_t), \ln(N_{t-1}), \ln(P_t), \ln(P_{t-1})) + \varepsilon_t \quad (2)$$

where N_t and N_{t-1} equal current and previous abundance of SPB, P_t and P_{t-1} abundance of *T. dubius*, and ε_t representing exogenous (density-independent) effects (e.g. due to weather and estimation error). Three model structures (Table 1) that incorporate predator or prey effects at different time lags were initially fit to data in each of the 95 forests. Akaike information criterion (AIC) and goodness-of-fit statistics of each model structure were compared to determine the model structure that best described SPB and *T. dubius* forest-scale dynamics across the southeastern USA. Support for the model describing SPB dynamics that included only direct effects of *T. dubius* abundance (P_t), for example, would suggest that *T. dubius* acts primarily as a generalist predator. A model structure including lagged abundances of *T. dubius* (P_{t-1}) would suggest a delayed response such as would be expected from a specialist natural enemy (Turchin 2003). Parameters from the best model structure were estimated for both species at each forest using the ‘nlme’ package in R (ver. 3.1.2). We then tested for significant spatial variation in each model parameter using a spline correlogram (Bjørnstad 2001) and estimated confidence intervals for the estimated functions with 1000 bootstrap resampling.

Spatial synchrony of population fluctuations of SPB and *T. dubius* across the southeastern USA

Spatial analyses were conducted to assess the average regional and local correlation (ρ at lag 0 minus average regional correlation), and the spatial extent (km) of the spatial autocorrelation in the population fluctuations of SPB and *T. dubius* across the 95 forests. Spatial nonparametric covariance functions were fit to ln-transformed abundances and growth rates (R_t) of SPB and *T. dubius* in each forest; region-wide correlations were estimated by the average Spearman rank correlation between all populations (Bjørnstad 2001). Spline correlograms were constructed to estimate spatial correlation in the mean ln-transformed abundances as a function of distance (Bjørnstad 2001). Lastly, we characterized the pattern of spatial cross-correlation between SPB and *T. dubius* by fitting spatial nonparametric cross-correlation functions (Bjørnstad and Bascompte 2001) for each of the demographic variables listed above. Confidence intervals for all estimated spatial correlation functions were calculated using bootstrap resampling (1000 bootstrapped samples). All spatial analyses were conducted using the ‘ncf’ package in R software (ver. 3.1.2).

Effects of forest composition on population stability of SPB and *T. dubius*

We hypothesized that spatial variation in the population dynamics of SPB and *T. dubius* across the southeastern USA was linked to local forest composition and structure. To test this we first assessed the spatial correlation among forests in pine basal area. We began by estimating average pine basal area for a circle with radius of 20 km around the center of each study forest. These values were extracted from a 1-km pine basal area raster (250-m) interpolated from standardized, regularly measured forest inventory plots throughout the U.S (Forest Inventory and Analysis (FIA) program of the USDA Forest Service; one plot every 2400 ha) using remotely-sensed and other physiographic variables as covariates (Blackard et al. 2008). We then used regression to estimate the influence of local pine forest basal area on equilibrium abundance of SPB and *T. dubius* estimated from the population model. Due to non-independence from spatial correlation, models with different spatial covariance structures were fit following procedures of Zuur et al. (2009) using the ‘nlme’ package in R (ver. 3.1.2); the best-fitting model was chosen based on AIC.

Table 1. Three model structures used to describe *Dendroctonus frontalis* (SPB) and *Thanasimus dubius* population dynamics within 95 forests across the southeastern USA.

Species	Model	Model structure
<i>Dendroctonus frontalis</i>	1	$R^N = \beta_0 + \beta_1 \times N_t + \beta_2 \times N_{t-1} + \varepsilon_t$
	2	$R^N = \beta_0 + \beta_1 \times N_t + \beta_2 \times P_t + \varepsilon_t$
	3	$R^N = \beta_0 + \beta_1 \times N_t + \beta_2 \times P_t + \beta_3 \times P_{t-1} + \varepsilon_t$
<i>Thanasimus dubius</i>	4	$R^P = \beta_0 + \beta_1 \times P_t + \beta_2 \times P_{t-1} + \varepsilon_t$
	5	$R^P = \beta_0 + \beta_1 \times P_t + \beta_2 \times N_t + \varepsilon_t$
	6	$R^P = \beta_0 + \beta_1 \times P_t + \beta_2 \times N_t + \beta_3 \times N_{t-1} + \varepsilon_t$

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.ms739>> (Weed et al. 2016).

Results

Geographical variation in temporal dynamics at the forest-scale

Population fluctuations of SPB and *T. dubius* were tightly coupled in time across the southeastern USA (Fig. 1) and the majority of autocorrelation functions of SPB and *T. dubius* decayed with increasing time lag suggesting populations were subjected to endogenous feedback. Autocorrelation functions also indicated that SPB and *T. dubius* dynamics at the forest-scale were primarily affected by abundance in the year prior (Fig. 2a, b). Delays in the feedback were suggested for some forests (e.g. in 27 forests for SPB and 44 for *T. dubius*), but there was no indication for periodicity in the dynamics of either species because ACF values at lags > 2 were never statistically significant (Bartlett's test; Turchin 2003, Guichard and Gouhier 2014).

Cross-correlation analysis indicated that synchrony in annual abundances of SPB and *T. dubius* is almost perfectly in phase in 65% of forests (i.e. highest correlation at time lag(0); Fig. 2c), but across the study region there was modest variation in the strength and pattern of temporal synchrony (Fig. 2c). In some forests, predator–prey fluctuations were also correlated at time lags greater than 0, but these correlations tended to be modest compared to the correlation at time lag(0). In general, *T. dubius* populations responded approximately instantaneously to annual SPB abundance.

Among the three alternative statistical models for temporal dynamics, the population dynamics of SPB and *T. dubius* were best described by the same model including immediate effects of the prey (N_t) and the predator (P_t) abundance, $R = \beta_0 + \beta_1 \times N_t + \beta_2 \times P_t + \epsilon_t$ (Table 1, models 2 and 5). Model fits (R^2 and p-value) and information content of this model structure consistently performed better than or as well as the alternative models (Supplementary material Appendix 1, Table A1 and A2). Model 2 provided an adequate fit ($p < 0.10$) to the SPB data within 65% (67 of 95) of the forests (average $R^2 = 0.31 \pm 0.02$, $n = 95$), for example, whereas models 1 and 3 provided satisfactory fits to the data in only 24% of the forests (average R^2 model 1: 0.23 ± 0.02 , model 3: 0.16 ± 0.02). Information content (AIC) of model 3 was consistently lower than either of the alternative models describing SPB dynamics (Supplementary material Appendix 1, Table A1). Similar results were found for comparisons of model fit to the *T. dubius* data (Supplementary material Appendix 1, Table A2). Information content of model 5 was higher or similar in 64 and 92% of forests compared models 4 and 6, respectively. Including the lagged effect of SPB abundance (N_{t-1}) in the model describing *T. dubius* dynamics (model 6) provided greater information content within only six forests compared to model 5. Model 5 provided consistently adequate fits ($p < 0.10$) to the *T. dubius* data in 77 of 95 forests (81%) with an average R^2 of 0.38 ± 0.02 , which was slightly better than the fits of models 4 ($p < 0.10$

in 61% forests, $R^2 = 0.31 \pm 0.02$) and 6 ($p < 0.10$ in 65% forests, $R^2 = 0.37 \pm 0.02$) (Supplementary material Appendix 1, Table A2).

Estimated coefficients from models 2 and 5, which measure the relative strength of demographic forces affecting temporal dynamics of SPB and *T. dubius* in each forest, varied widely across the southeastern USA (Fig. 3 and 4, Supplementary material Appendix 1, Fig. A1). Density-dependent and density-independent factors affecting forest-scale dynamics were generally uncorrelated in space across the study region (Fig. 3 and 4, Table 2) but there was significant spatial correlation in estimates of *T. dubius* maximum population growth rate (intercept term) among forests (Fig. 4a and Table 2).

The effect of prior SPB (β_1) abundance on *D. frontalis* population growth across the southeast USA was predominantly negative (95% of forests) and averaged -0.59 ± 0.42 (mean \pm SD). Despite this, the strength of negative feedback from prior SPB abundance was not spatially correlated across the study region (Fig. 3b). Feedback from prior *T. dubius* abundance (β_2) was also, on average, negative (-0.18 ± 0.85), but models estimated the effect to be greater than zero in 40% of the forests (Supplementary material Appendix 1, Table A3 and Fig. A1). This suggests that the effect of *T. dubius* abundance on long-term SPB dynamics is highly variable across the southeast USA and generally uncorrelated, at least beyond approximately 30 km (Fig. 3c).

Model estimates indicated that population growth of *T. dubius* responded, on average, positively to prior abundance of SPB (β_1 : 0.17 ± 0.25) while prior *T. dubius* abundance tended to reduce population growth (β_2 : -0.94 ± 0.35) (Supplementary material Appendix 1, Table A4 and Fig. A1). Exogenous effects were not spatially correlated (Fig. 4d), but the maximum population growth rate (intercept term) of *T. dubius* was correlated up to approximately 400 km (Fig. 4a and Table 2).

Spatial synchrony of SPB and *T. dubius* across the southeastern USA

Population fluctuations of SPB and *T. dubius* across the entire southeastern USA were correlated at similar spatial scales (i.e. over 400 km, a quarter of the maximum distance between forests) (Fig. 5 and Table 3). Spatial correlations of the ln-abundances and growth rates were similar for both species so correlations in ln-abundances are only shown in Fig. 5. Interannual growth rates, annual abundance, and the long-term mean abundance of both species were correlated at the local scale (y-intercept or lag distance = 0 km) indicating strong interspecific synchrony in temporal dynamics among closely located forests (Table 3). Local correlation was higher for *D. frontalis* abundance compared to *T. dubius* but growth rates were only marginally higher for SPB compared to *T. dubius* (Table 3). Regional average correlations of the space-time abundance and growth rate estimates were similar for both species (averaged 0.19) (Fig. 5 and Table 3). Spatial correlation in the long-term mean abundances, however, declined rapidly with distance (Fig. 5 and Table 3).

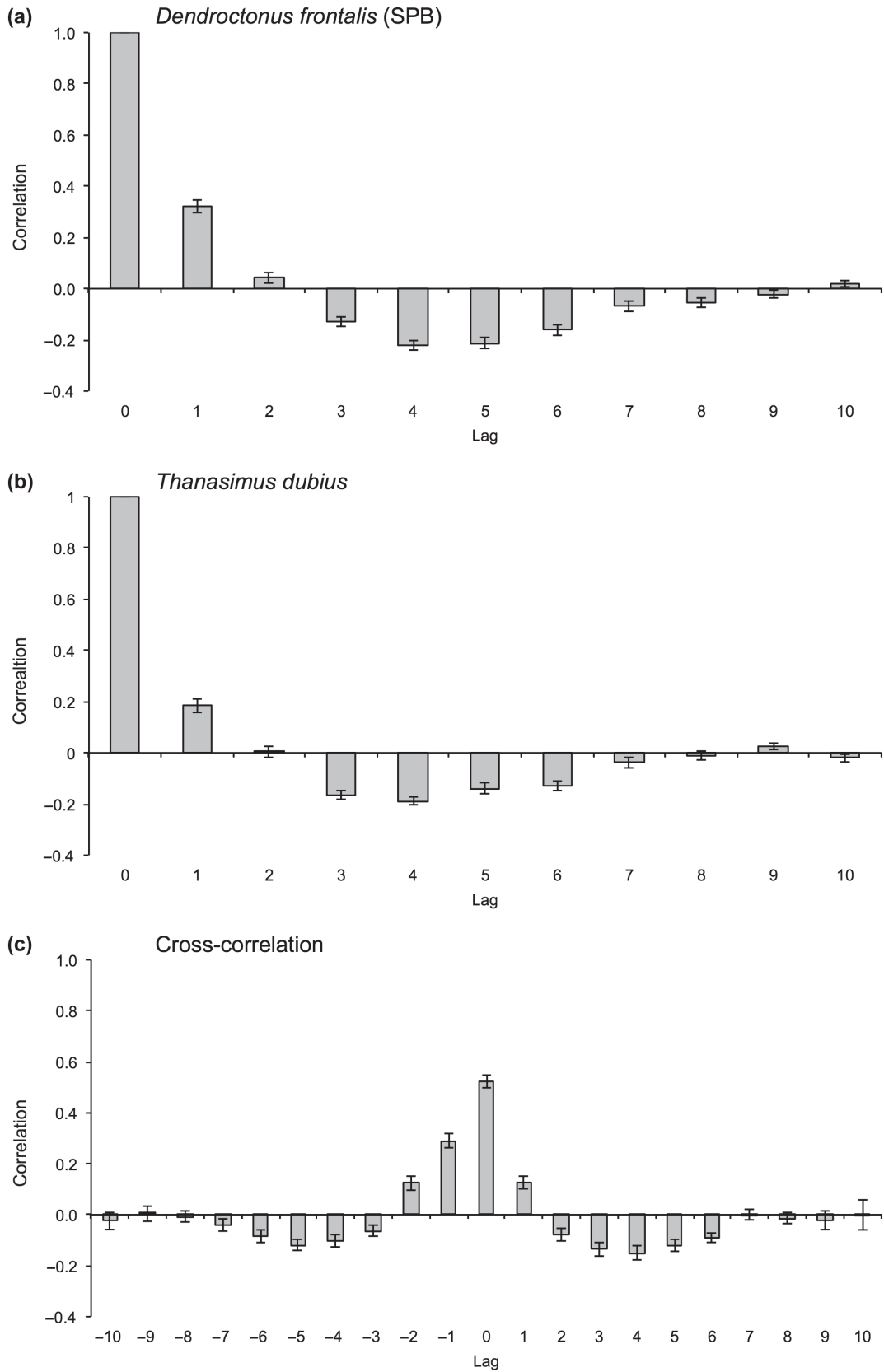


Figure 2. Average autocorrelation (ACF) functions estimated from 95 time series of (a) *Dendroctonus frontalis* (SPB) and (b) *Thanasimus dubius* abundances and (c) their cross-correlation (CCF) across the southeastern USA. Bars denote mean values \pm SE.

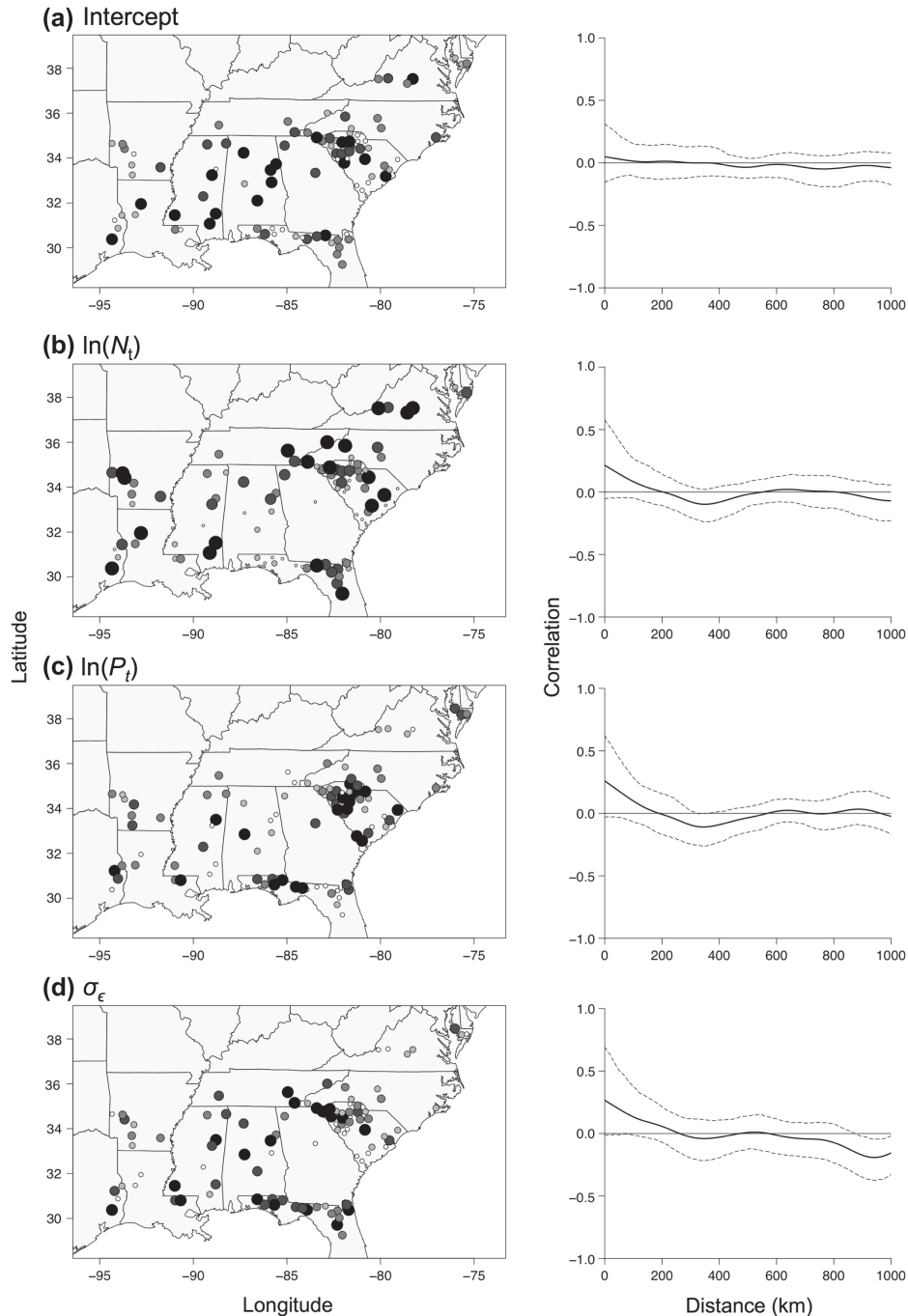


Figure 3. Spatial distribution (left panels) and correlation (right panels) of estimated model coefficients describing local dynamics of *Dendroctonus frontalis* (SPB). Dot shading and size correspond to the quintiles of coefficient values where smaller coefficient values are indicated by small, lighter shaded dots and large values indicated by dark, large dots. Confidence intervals (dashed lines) for the estimated functions (solid lines) were calculated using 1000 bootstrap resampling.

Effects of forest composition on population stability of SPB and *T. dubius*

Host (*Pinus* spp.) basal area within 20-km circular buffers around each forest district averaged 23.6 m² ha⁻¹ across the study region and was correlated beyond 200 km (Fig. 6a, b). Loblolly pine *P. taeda* was the most common species, accounting for 75% of the basal area. Shortleaf *P. echinata* and Virginia *P. virginiana* pines were the next

most common species, representing 8% of the pine basal area. After accounting for spatial dependence, the long-term average abundance of SPB (Fig. 6c) was positively related to pine forest basal area within 20 km around each forest district ($F = 4.3$; $DF = 1, 93$; $p = 0.04$); the same relationship was only marginally significant for *T. dubius* ($F = 3.5$; $DF = 1, 93$; $p = 0.07$). Spatial variation in the abundance of *T. dubius* across the region, however, was best explained by average SPB abundance ($F = 69.1$; $DF = 1, 93$; $p < 0.01$) (Fig. 6d).

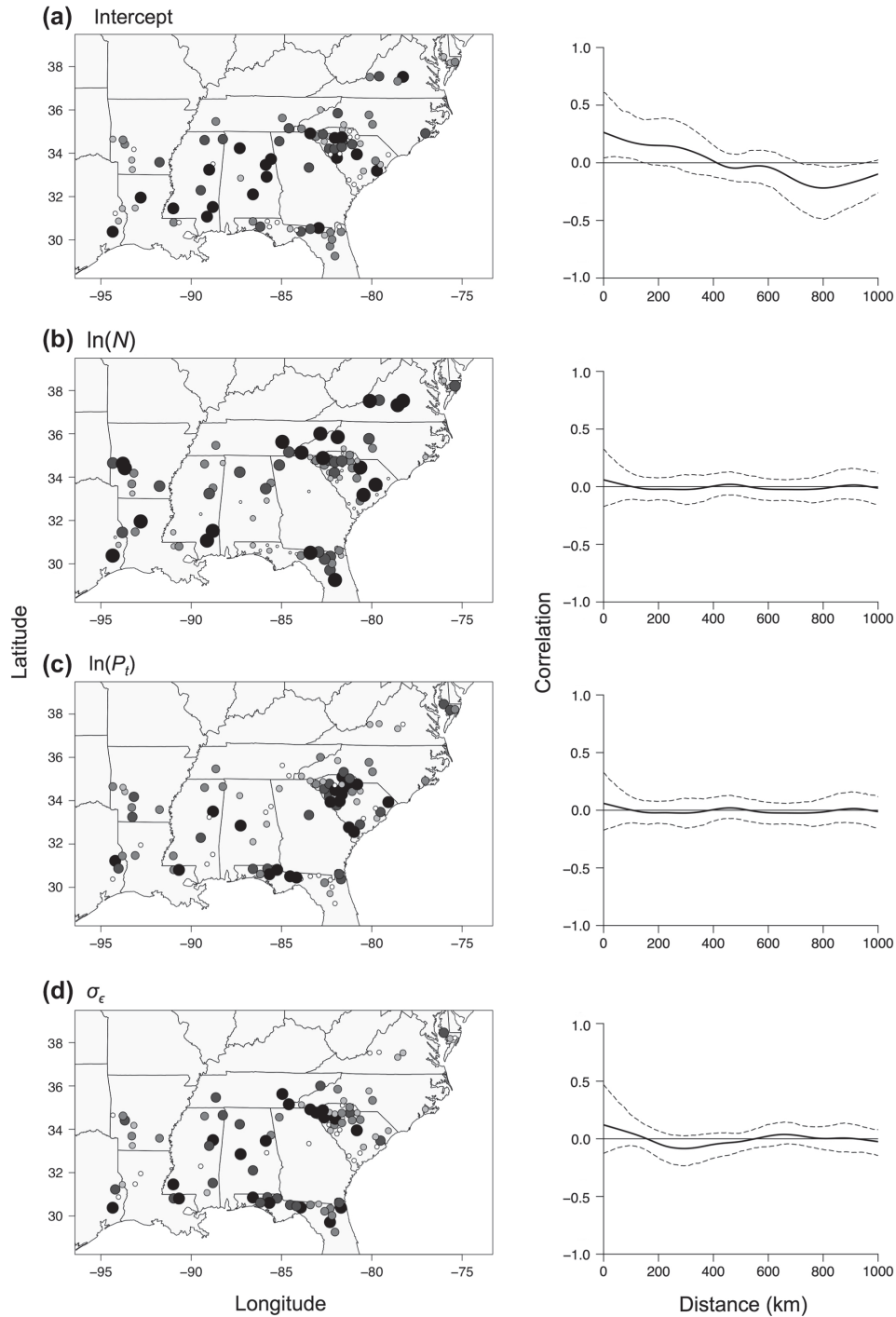


Figure 4. Spatial distribution (left panels) and correlation (right panels) of estimated model coefficients describing local dynamics of *Thanasimus dubius*. Dot shading and size correspond to the quintiles of coefficient values where smaller coefficient values are indicated by small, lighter shaded dots and large values indicated by dark, large dots. Confidence intervals (dashed lines) for the estimated functions (solid lines) were calculated using 1000 bootstrap resampling.

Table 2. Estimates (\pm 95% bootstrap CI) of the local autocorrelation and distance at which the spatial correlation (ρ) becomes zero for model coefficients describing temporal dynamics of *Dendroctonus frontalis* (SPB) and *Thanasimus dubius* within 95 forests.

Model coefficients	<i>Dendroctonus frontalis</i> (SPB)		<i>Thanasimus dubius</i>	
	Local autocorrelation (ρ)	x-intercept (km)	Local autocorrelation (ρ)	x-intercept (km)
Intercept	0.05 [-0.16, 0.31]	307 [-559, 462]	0.26 [0.05, 0.66]	412 [159, 655]
$\ln(N_t)$	0.21 [-0.05, 0.58]	204 [-268, 372]	0.06 [-0.20, 0.36]	104 [-496, 528]
$\ln(P_t)$	0.26 [-0.03, 0.62]	190 [-145, 306]	0.05 [-0.22, 0.35]	89 [-429, 592]
σ_ϵ	0.27 [-0.01, 0.69]	262 [-37, 693]	0.12 [-0.14, 0.44]	158 [-558, 330]

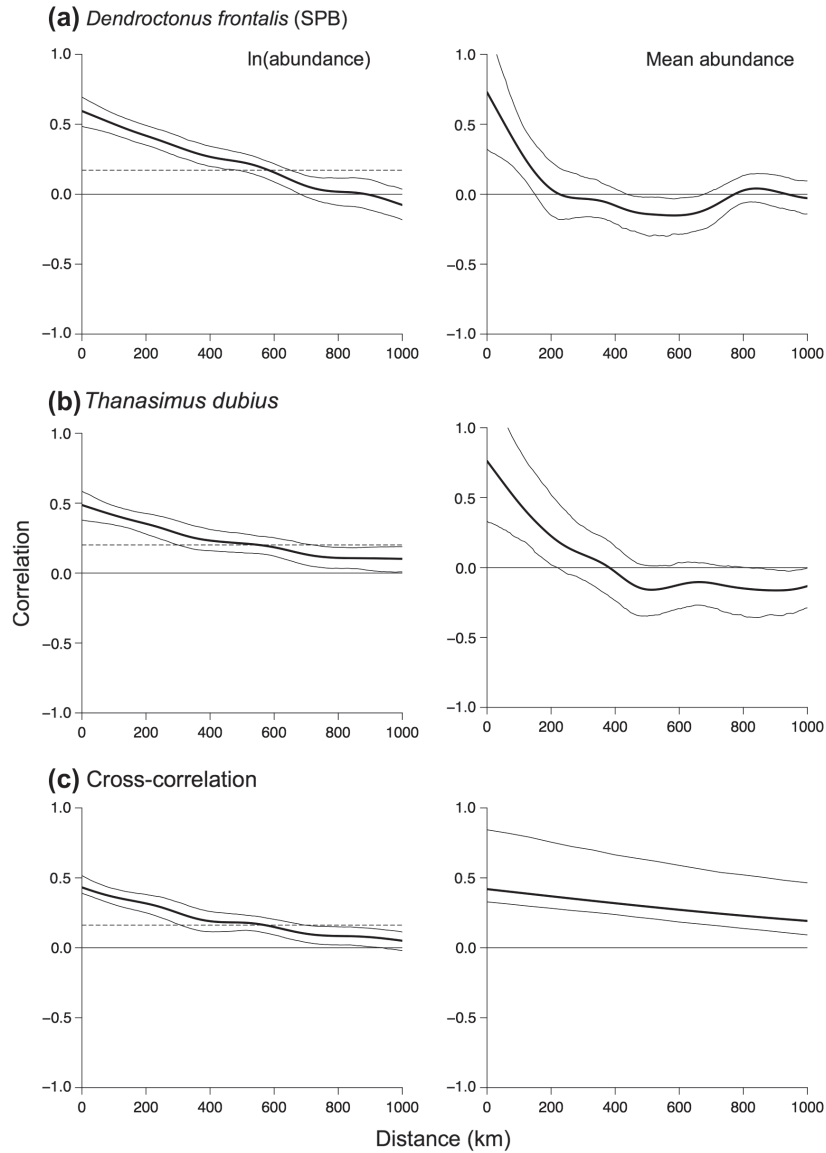


Figure 5. Spatial nonparametric correlation functions for four variables describing (a) *Dendroctonus frontalis* (SPB) and (b) *Thanasimus dubius* dynamics and (c) their spatial cross-correlation. Solid, black lines denote estimated mean correlation functions with 95% bootstrapped CI (gray lines). Dashed line denotes regional correlation estimated from space-time ln(abundance).

Discussion

Linkages between local-scale processes to regional-scale patterns in abundance of interacting species are limited

because data are often unavailable for widely-distributed populations. As a consequence, most treatments addressing whether spatial variation in population dynamics at the landscape-scale is an emergent property of spatially

Table 3. Estimates (\pm 95% bootstrap CI) of the regional average, local autocorrelation, and distance at which the spatial correlation (ρ) becomes zero for four demographic variables describing dynamics of *Dendroctonus frontalis* (SPB) and *Thanasimus dubius* and their spatial cross-correlation. Refer to Fig. 5 for plotted correlation functions.

Species	Measure of spatial correlation	ln (abundance)	Growth rate (R)	Mean ln (abundance) per forest
<i>Dendroctonus frontalis</i> (SPB)	Regional correlation	0.17 [0.12, 0.23]	0.13 [0.10, 0.17]	–
	Local autocorrelation	0.42 [0.32, 0.53]	0.35 [0.25, 0.45]	0.73 [0.32, 1.23]
	Distance (km)	583 [476, 655]	464 [379, 563]	226 [149, 404]
<i>Thanasimus dubius</i>	Regional correlation	0.20 [0.15, 0.25]	0.11 [0.07, 0.14]	–
	Local autocorrelation	0.29 [0.18, 0.39]	0.25 [0.13, 0.35]	0.76 [0.33, 1.37]
	Distance (km)	552 [280, 713]	493 [385, 747]	381 [218, 493]
Cross-correlation	Regional correlation	0.16 [0.12, 0.22]	0.08 [0.05, 0.11]	–
	Local autocorrelation	0.26 [0.22, 0.35]	0.19 [0.16, 0.31]	0.42 [0.33, 0.83]
	Distance (km)	568 [296, 704]	434 [308, 817]	11,779 [1650, 12381]

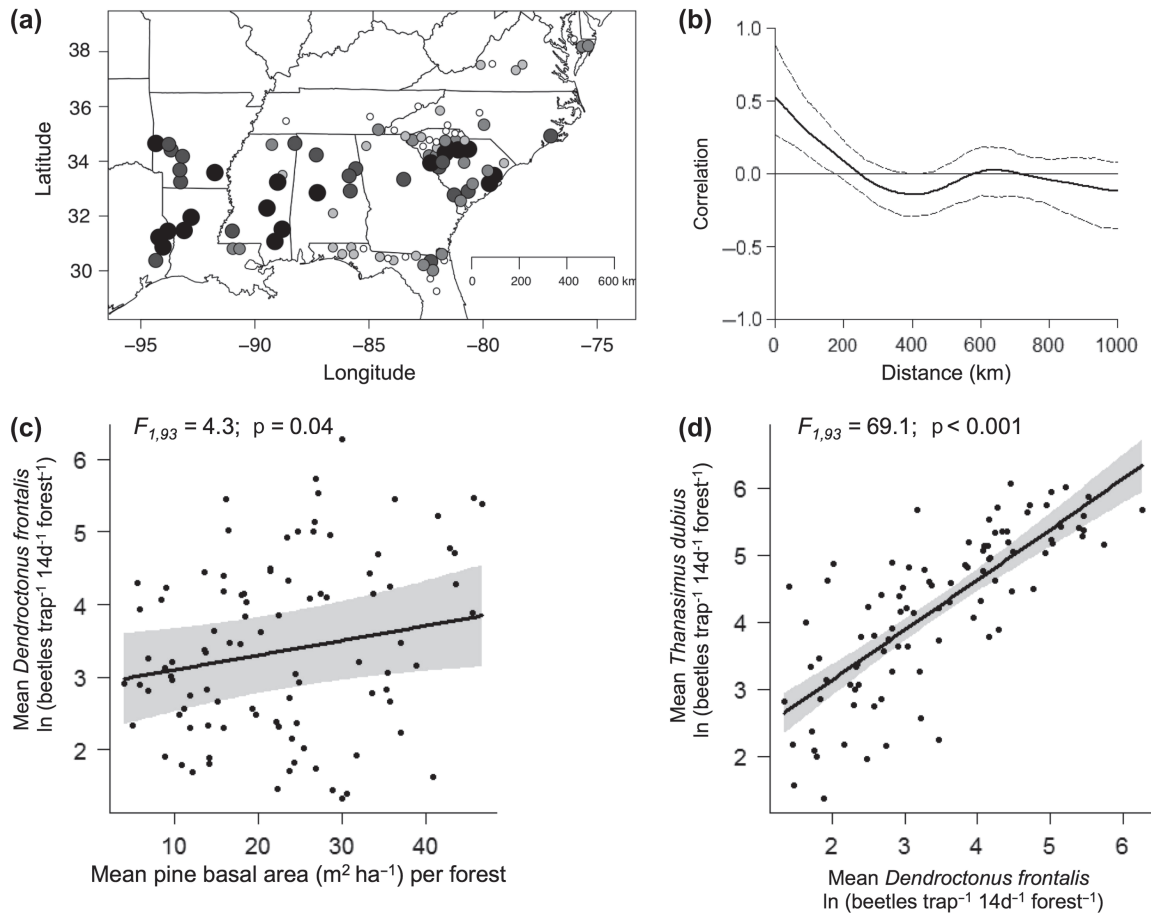


Figure 6. Spatial distribution (a) and correlation (b) of *Pinus* basal average ($\text{m}^2 \text{ha}^{-1}$) in 20 km circular buffers surrounding each forest. The long-term abundance of *Dendroctonus frontalis* (SPB) and *Thanosimus dubius* is related to the spatial variation in *Pinus* basal area (c) and *Dendroctonus frontalis* abundance (d), respectively. Dot shading and size on map correspond to the quintiles of basal area values. Forests with smaller mean basal areas are denoted by small, lighter shaded dots and large basal area values denoted by dark, large dots. Shading around regression line represents standard error confidence intervals.

structured trophic interactions or linked to variation in resource quality are theoretical (Hassell et al. 1991, Bjørnstad and Bascompte 2001, Cronin and Reeve 2005, Riolo et al. 2015). Using a broad network of intensively sampled forests across the southeastern USA, we estimated the distance at which the dynamics between the southern pine beetle and its key predator covary in space and measured spatial patterns in the deterministic and stochastic processes affecting this predator-prey system at the local, forest-scale. As expected, we found that the population dynamics of these interacting species sampled annually are linked tightly in time and space. Surprisingly, however, the deterministic and stochastic processes responsible for generating forest-scale fluctuations of SPB and *T. dubius* were overwhelmingly uncorrelated in space. Spatial variation in long-term forest-scale abundance was linked most strongly to the abundance (basal area of pine) of potential habitat indicating a stronger role for resource availability on SPB population dynamics than top-down effects.

Spatial synchrony of SPB abundance and growth rates were similar to that reported in a previous study (Økland et al. 2005), but our estimates of local and regional correlation were generally lower. The higher level of synchrony reported from county-level data in Økland et al. (2005)

most likely reflects a sample unit size effect (Dungan et al. 2002). The pattern of declining synchrony with lag distance, observed here for both SPB and *T. dubius*, parallels the general pattern observed across diverse taxonomic groups of animals (Liebhold et al. 2004). Spatial synchrony of SPB (~ 500 km) is also similar to other reported examples of bark beetles, which as a group tends to be lower than Lepidoptera (Peltonen et al. 2002, Bjørnstad 2003, Økland et al. 2005, Aukema et al. 2006). For instance, Peltonen et al. (2002) reported spatial synchrony of gypsy moth and spruce budworm to exceed 600 and 1000 km, respectively.

Our multiple analyses clearly demonstrate that population dynamics of SPB and *T. dubius* are correlated over a large geographic distance (> 500 km). In spite of this strong spatial structure, there was little indication of either a temporal or spatial lag in the response of *T. dubius* to annual SPB abundance. In biological terms, there is little or no temporal delay in the response of *T. dubius* to annual SPB density. This is in contrast to prior studies that evaluated generational mortality of SPB due to *T. dubius* (Turchin et al. 1999) and other systems where natural enemies are hypothesized to lag their host in time and space as observed for the larch budmoth and autumnal moth in Europe (Bjørnstad et al. 2002, Tenow et al. 2007). Given that the generation time of

T. dubius is longer than that of SPB (Reeve 2011), the lack of a temporal lag from a change in annual SPB abundance to an annual change in the abundance of its predator indicates a functional rather than numerical response, which implies that *T. dubius* acts more as a generalist predator rather than a specialist (Hanski et al. 1991, Turchin 2003).

Spatial synchrony is commonly attributed to spatially synchronous stochastic effects (e.g. weather; Moran 1953) or movement of hosts and/or their natural enemies (Ydenberg 1987, Ims and Steen 1990, Kendall et al. 2000). However, the relative importance of regional vs local processes in synchronizing populations in space depends greatly on the strength of the interacting, often nonlinear, feedback system (Royama 2005, Vasseur and Fox 2009). For example, only weak exogenous effects may only be occasionally required to synchronize fluctuations of cyclical species (Moran 1953) and mobile natural enemies may enhance synchrony of cyclical species through their dispersal to areas of peak abundance (Ydenberg 1987, Ims and Steen 1990). Our analyses support the view that population fluctuations of SPB are not cyclical as previously suggested (Turchin et al. 1991, 1999). In 95 time series distributed over most of the range of SPB in the U.S., there were only a few cases with even a weak signal of periodicity. Furthermore, the feedbacks between SPB and its chief predator, *T. dubius*, although strong, lacked evidence of the delays that are the general cause of population cycles (Supplementary material Appendix 1, Table A1 and A2; Berryman 2002, Turchin 2003). There was instead strong support for a model including direct effects from *T. dubius* acting with an almost instantaneous response to annual SPB abundance. Trapping and observational studies confirm that *T. dubius* does not typically go locally extinct when SPB is absent or rare, presumably because it can maintain a stable population on other conifer-attacking bark beetle species (e.g. *Ips* spp.; Martinson et al. 2013). Perhaps this stability and host-switching behavior of *T. dubius* explains why its spatial synchrony is comparable to that of SPB, whereas spatial synchrony of specialist natural enemies tends to be lower than that of their hosts (Satake et al. 2004).

The lack of cyclical tendencies in SPB implies a more active role for geographically broad exogenous effects on populations (e.g. from climatic patterns; Ungerer et al. 1999, Tr  n et al. 2007). Fluctuations in SPB abundance seem to be the result of stochastic switches between low and high abundances (Mawby and Gold 1984, Martinson et al. 2013). Therefore, compared to cyclical populations, more frequent exogenous forcing would be required to synchronize populations over large areas. Demographic effects from temperature, such as the influence of cold on winter survival or seasonal temperatures on development, might play a role in synchronizing SPB populations (Ungerer et al. 1999, Tr  n et al. 2007, Duehl et al. 2011). Precipitation has regional-scale effects on tree productivity and defense that might be important to synchronizing populations of some bark beetles (Bj  rnstad 2003, Raffa et al. 2008), but this does not seem to be the case for SPB (Turchin et al. 1991, McNulty et al. 1997). In fact, the resin defenses in loblolly pine are actually elevated at moderate levels of drought (Lorio 1986, Lombardero et al. 2000). Synchrony of SPB could however be influenced from rainfall influencing the phloem resource

for developing SPB brood (Gumpertz and Pye 2000, Duehl et al. 2011).

The parameter estimates describing temporal dynamics of annual SPB and *T. dubius* abundances varied substantially across the study region and lacked any signs of spatial patterning among National Forests and other trapping sites. *Thanasimus dubius* is generally regarded as a factor in suppressing SPB outbreaks (Reeve 2011). In fact, its abundance relative to SPB in spring trap captures is used as predictor of SPB risk (Billings and Upton 2010). Our results indicate that local impacts by *T. dubius* on SPB are somewhat context dependent. In general, prior *T. dubius* abundance negatively influenced SPB growth rates but this effect ranged across forests from weakly positive to strongly negative (and never spatially correlated beyond 30 km). There was a similar spatio-temporal structure to effects of prior SPB abundance on its own growth rates and those of *T. dubius*. Spatial structure in the temporal dynamics must exist at smaller scales via dispersal (Turchin and Thoeny 1993, Cronin et al. 2000, Friedenberget al. 2007a), but it is relevant to assessing outbreak risk of forest stands to SPB and our understanding of the biology that the spatial linkages decay within < 30 km.

Geographical variation in population dynamics is probably common, reported in the European spruce beetle *Ips typographus* (Bj  rnstad 2003), multiple outbreaking Lepidoptera (Volney and McCullough 1994, Williams and Liebhold 2000, Johnson et al. 2006, Klemola et al. 2006, Liebhold et al. 2006, Bj  rnstad et al. 2010), a midge (Choi et al. 2011), rodents (Bj  rnstad et al. 1995), and large ungulates (Post 2005). In some of these systems, the causes of the geographical patterning are reasonably well understood. For instance, geographical gradients in the dynamics of small rodents in Sweden (Hanski et al. 1991, Bj  rnstad et al. 1995, Hanski et al. 2001) are linked to spatial gradients in natural enemy composition, and population dynamics of *I. typographus* in Norway and of ungulates in Greenland, Finland, and Russia display a strong latitudinal trend (Bj  rnstad 2003, Post 2005). In our system, increases in local abundance of the basal resource, pine, was related to increases in the equilibrium abundances of SPB and *T. dubius*. Host availability, and probably its configuration in the landscape (Roland et al. 1998, Ylloja et al. 2005), must be of common importance in the population dynamics of many forest insects (Haynes et al. 2009). Our results support the general hypothesis that basal resources can shape the spatial and temporal interactions between predators and their prey (Cronin and Reeve 2005, Tscharrntke et al. 2005, Riolo et al. 2015).

Spatial patterns of closely-interacting species, including predator-prey systems, are a product of individual demographic rates, dispersal, the strength and form of interaction functions, and local stochastic effects (Hassell et al. 1991, Bj  rnstad and Bascompte 2001, Tobin and Bj  rnstad 2003). Collectively, these factors govern the temporal and spatial lags at which a natural enemy, for example, tends to respond to prey density (Rossi and Fowler 2003, Tobin and Bj  rnstad 2003, Satake et al. 2004) and the spatial scale at which behavioral and demographic rates are influenced. Recognition of scale effects has proven important to our understanding of natural enemy and pollinator services in agricultural systems (Tscharrntke et al. 2005, Gardiner et al.

2009) and contributed to our general understanding of the scale at which density-dependent vs density-independent events affect demography of populations (Post 2005). The emerging view from this and many systems is that animal populations tend to be synchronized in space via spatially correlated processes like weather (Liebhold et al. 2004), yet local dynamics, such as the periodicity of outbreaks, tend to be linked strongly to smaller scale host patterns (Haynes et al. 2012). Results presented here suggest that outbreaks are most likely synchronized by weather but also that local forest composition dictates interactions among multiple, often non-linear processes at the local scale.

Acknowledgements – We thank cooperators and Texas A&M Forest Service for coordinating and maintaining the southern pine beetle trapping network. Carla Pimentel, Carissa Aoki, and Jeff Lombardo helped with data management. The Southern Research Station, USDA Forest Service, provided financial support. Thanks to Ken Raffa for his critiques, questions, and suggestions.

References

- Aukema, B. H. et al. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. – *Ecography* 29: 427–441.
- Bellamy, P. et al. 2003. Synchrony of woodland bird populations: the effect of landscape structure. – *Ecography* 26: 338–348.
- Berryman, A. A. 2002. Population cycles: the case for trophic interactions. – Oxford Univ. Press.
- Berryman, A. A. 2003. On principles, laws and theory in population ecology. – *Oikos* 103: 695–701.
- Billings, R. F. and Upton, W. W. 2010. A methodology for assessing annual risk of southern pine beetle outbreaks across the southern region using pheromone traps. – In: Pye, J. M. et al. (eds), *Advances in threat assessment and their application to forest and rangeland management*. Gen. Tech. Rep. PNW-GTR-802, Portland, OR, U.S. Dept of Agriculture, Forest Service, Pacific Northwest and Southern Research Stations, pp. 73–85.
- Bjørnstad, O. N. 2001. Nonparametric spatial covariance functions: estimation and testing. – *Environ. Ecol. Stat.* 8: 53–70.
- Bjørnstad, O. N. 2003. Synchrony and geographical variation of the spruce bark beetle (*Ips typographus*) during a non-epidemic period. – *Popul. Ecol.* 45: 213–219.
- Bjørnstad, O. N. and Bascompte, J. 2001. Synchrony and second-order spatial correlation in host-parasitoid systems. – *J. Anim. Ecol.* 70: 924–933.
- Bjørnstad, O. N. et al. 1995. A geographic gradient in small rodent density fluctuations: a statistical modelling approach. – *Proc. R. Soc. B* 262: 127–133.
- Bjørnstad, O. N. et al. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. – *Trends Ecol. Evol.* 14: 427–432.
- Bjørnstad, O. N. et al. 2002. Waves of larch budmoth outbreaks in the European alps. – *Science* 298: 1020–1023.
- Bjørnstad, O. N. et al. 2010. Geographic variation in North American gypsy moth cycles: subharmonics, generalist predators, and spatial coupling. – *Ecology* 91: 106–118.
- Blackard, J. et al. 2008. Mapping U.S. forest biomass using nationwide forest inventory data and moderate resolution information. – *Remote Sens. Environ.* 112: 1658–1677.
- Borcard, D. et al. 2004. Dissecting the spatial structure of ecological data at multiple scales. – *Ecology* 85: 1826–1832.
- Choi, W. I. et al. 2011. Geographical variation in the population dynamics of *Thecodiplosis japonensis*: causes and effects on spatial synchrony. – *Popul. Ecol.* 53: 429–439.
- Cronin, J. and Reeve, J. 2005. Host–parasitoid spatial ecology: a plea for a landscape-level synthesis. – *Proc. R. Soc. B* 272: 2225.
- Cronin, J. T. et al. 2000. The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. – *Oikos* 90: 127–138.
- Duehl, A. J. et al. 2011. Southern pine beetle regional outbreaks modeled on landscape, climate and infestation history. – *For. Ecol. Manage.* 261: 473–479.
- Dungan, J. L. et al. 2002. A balanced view of scale in spatial statistical analysis. – *Ecography* 25: 626–640.
- Erbilgin, N. and Raffa, K. F. 2001. Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. – *Oecologia* 127: 444–453.
- Friedenberg, N. A. et al. 2007a. Synchrony's double edge: transient dynamics and the Allee effect in stage structured populations. – *Ecol. Lett.* 10: 564–573.
- Friedenberg, N. A. et al. 2007b. Differential impacts of the southern pine beetle, *Dendroctonus frontalis*, on *Pinus palustris* and *Pinus taeda*. – *Can. J. For. Res.* 37: 1427–1437.
- Friedenberg, N. A. et al. 2008. Temperature extremes, density dependence, and southern pine beetle (Coleoptera: Curculionidae) population dynamics in east Texas. – *Environ. Entomol.* 37: 650–659.
- Gardiner, M. M. et al. 2009. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. – *Ecol. Appl.* 19: 143–154.
- Grøtan, V. et al. 2009. Geographical variation in the influence of density dependence and climate on the recruitment of Norwegian moose. – *Oecologia* 161: 685–695.
- Guichard, F. and Gouhier, T. C. 2014. Non-equilibrium spatial dynamics of ecosystems. – *Math. Biosci.* 255: 1–10.
- Gumpertz, L. and Pye, M. 2000. Logistic regression for southern pine beetle outbreaks with spatial and temporal autocorrelation. – *For. Sci.* 46: 95–107.
- Hanski, I. et al. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. – *J. Anim. Ecol.* 60: 353–367.
- Hanski, I. et al. 2001. Small-rodent dynamics and predation. – *Ecology* 82: 1505–1520.
- Hassell, M. et al. 1991. Spatial structure and chaos in insect population dynamics. – *Nature* 353: 255–258.
- Haynes, K. J. et al. 2007. Landscape context outweighs local habitat quality in its effects on herbivore dispersal and distribution. – *Oecologia* 151: 431–441.
- Haynes, K. J. et al. 2009. Spatial analysis of harmonic oscillation of gypsy moth outbreak intensity. – *Oecologia* 159: 249–256.
- Haynes, K. J. et al. 2012. Geographical variation in the spatial synchrony of a forest-defoliating insect: isolation of environmental and spatial drivers. – *Proc. R. Soc. B* 280: 20122373.
- Hofstetter, R. et al. 2006. Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. – *Oecologia* 147: 679–691.
- Ims, R. A. and Steen, H. 1990. Geographical synchrony in microtine population cycles: a theoretical evaluation of the role of nomadic avian predators. – *Oikos* 57: 381–387.
- Johnson, D. M. et al. 2006. Geographical variation in the periodicity of gypsy moth outbreaks. – *Ecography* 29: 367–374.
- Kendall, B. et al. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. – *Am. Nat.* 155: 628–636.
- Klemola, T. et al. 2006. Geographically partitioned spatial synchrony among cyclic moth populations. – *Oikos* 114: 349–359.
- Kruess, A. 2003. Effects of landscape structure and habitat type on a plant–herbivore–parasitoid community. – *Ecography* 26: 283–290.

- Lambin, X. 1998. Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. – *Proc. R. Soc. B* 265: 1491–1496.
- Li, L. and Jin, Z. 2011. Pattern dynamics of a spatial predator–prey model with noise. – *Nonlinear Dyn.* 67: 1737–1744.
- Lih, M. P. and Stephen, F. M. 1996. Relationship of host tree diameter to within-tree southern pine beetle (Coleoptera: Scolytidae) population dynamics. – *Environ. Entomol.* 25: 736–742.
- Liebold, A. M. et al. 2004. Spatial synchrony in population dynamics. – *Annu. Rev. Ecol. Evol. Syst.* 35: 467–490.
- Liebold, A. M. et al. 2006. Geographic variation in density-dependent dynamics impacts the synchronizing effect of dispersal and regional stochasticity. – *Popul. Ecol.* 48: 131–138.
- Lombardero, M. et al. 2000. Environmental effects on constitutive and inducible resin defences of *Pinus taeda*. – *Ecol. Lett.* 3: 329–339.
- Lorio, J. P. L. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle–tree interactions. – *For. Ecol. Manage.* 14: 259–273.
- Martinson, S. et al. 2007. Why does longleaf pine have low susceptibility to southern pine beetle? – *Can. J. For. Res.* 37: 1966–1977.
- Martinson, S. J. et al. 2013. Alternate attractors in the population dynamics of a tree-killing bark beetle. – *Popul. Ecol.* 55: 95–106.
- Mawby, W. D. and Gold, H. J. 1984. A reference curve and space-time series analysis of the regional population-dynamics of the southern pine-beetle (*Dendroctonus frontalis* Zimmermann) (Coleoptera, Scolytidae). – *Popul. Ecol.* 26: 261–274.
- McNulty, S. et al. 1997. Predictions of southern pine beetle populations under historic and projected climate using a forest ecosystem model. – In: Mickler, R. A. and Fox, S. (eds), *The productivity and sustainability of southern forest ecosystems in a changing environment*. Springer, pp. 617–634.
- Meddens, A. J. H. et al. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. – *Ecol. Appl.* 22: 1876–1891.
- Moran, P. 1953. The statistical analysis of the canadian lynx cycle. 2. Synchronization and meteorology. – *Aust. J. Zool.* 1: 291–298.
- Nixon, A. E. and Roland, J. 2012. Generalist predation on forest tent caterpillar varies with forest stand composition: an experimental study across multiple life stages. – *Ecol. Entomol.* 37: 13–23.
- Økland, B. et al. 2005. Are bark beetle outbreaks less synchronous than forest Lepidoptera outbreaks? – *Oecologia* 146: 365–372.
- Payne, T. et al. 1984. Insect predator–prey coevolution via enantiomeric specificity in a kairomone-pheromone system. – *J. Chem. Ecol.* 10: 487–492.
- Peltonen, M. et al. 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. – *Ecology* 83: 3120–3129.
- Post, E. 2005. Large-scale spatial gradients in herbivore population dynamics. – *Ecology* 86: 2320–2328.
- Raffa, K. F. et al. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. – *Bioscience* 58: 501–517.
- Ranta, E. et al. 1997. Dynamics of Canadian lynx populations in space and time. – *Ecography* 20: 454–460.
- Reeve, J. 1997. Predation and bark beetle dynamics. – *Oecologia* 112: 48–54.
- Reeve, J. D. 2011. Predators of the southern pine beetle. – In: Coulson, R. N. and Klepzig, K. D. (eds), *Southern pine beetle II. Gen. Tech. Rep. SRS-140*, USDA Forest Service, Southern Research Station, pp. 153–160.
- Reeve, J. D. and Turchin, P. 2002. Evidence for predator–prey cycles in a bark beetle. – In: Berryman, A. A. (ed.), *Population cycles: the case for trophic interactions*. Oxford Univ. Press, pp. 92–108.
- Riolo, M. A. et al. 2015. Local variation in plant quality influences large-scale population dynamics. – *Oikos* 124: 1160–1170.
- Roland, J. and Taylor, P. D. 1997. Insect parasitoid species respond to forest structure at different spatial scales. – *Nature* 386: 710–713.
- Roland, J. et al. 1998. Effects of climate and forest structure on duration of forest tent caterpillar outbreaks across central Ontario, Canada. – *Can. Entomol.* 130: 703–714.
- Rossi, M. and Fowler, H. 2003. The sugarcane borer *Diatraea saccharalis* (Fabr.) (Lep., Crambidae) and its parasitoids: a synchrony approach to spatial and temporal dynamics. – *J. Appl. Entomol.* 127: 200–208.
- Royama, T. 1992. *Analytical population dynamics*. – Chapman and Hall.
- Royama, T. 2005. Moran effect on nonlinear population processes. – *Ecol. Monogr.* 75: 277–293.
- Satake, A. et al. 2004. Masting and trophic cascades: interplay between rowan trees, apple fruit moth, and their parasitoid in southern Norway. – *Oikos* 104: 540–550.
- Tenow, O. et al. 2007. Waves and synchrony in *Epirrita autumnata*/*Operophtera brumata* outbreaks. I. Lagged synchrony: regionally, locally and among species. – *J. Anim. Ecol.* 76: 258–268.
- Thatcher, R. C. (ed.) 1980. *The southern pine beetle*. – Technical Bulletin 1631, United States Dept of Agriculture Forest Service, Combined Forest Pest Research and Development Program, Pineville, LA.
- Thies, C. et al. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. – *Oikos* 101: 18–25.
- Tobin, P. C. and Bjørnstad, O. N. 2003. Spatial dynamics and cross-correlation in a transient predator–prey system. – *J. Anim. Ecol.* 72: 460–467.
- Trần, J. et al. 2007. Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis*. – *Ecol. Appl.* 17: 882–899.
- Tscharntke, T. et al. 2005. The landscape context of trophic interactions: insect spillover across the crop–noncrop interface. – *Ann. Zool. Fenn.* 42: 421–432.
- Turchin, P. 2003. *Complex population dynamics: a theoretical/empirical synthesis*. – Princeton Univ. Press.
- Turchin, P. and Thoeny, W. T. 1993. Quantifying dispersal of southern pine beetles with mark–recapture experiments and a diffusion model. – *Ecol. Appl.* 187–198.
- Turchin, P. et al. 1991. Why do populations of southern pine beetles (Coleoptera, Scolytidae) fluctuate? – *Environ. Entomol.* 20: 401–409.
- Turchin, P. et al. 1997. Spatial pattern formation in ecological systems: bridging theoretical and empirical approaches. – In: Bascompte, J. and Sole, R. V. (eds), *Modeling spatiotemporal dynamics in ecology*. Springer, pp. 19–213.
- Turchin, P. et al. 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. – *Science* 285: 1068–1071.
- Ungerer, M. J. et al. 1999. Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). – *J. Biogeogr.* 26: 1133–1145.
- Vasseur, D. A. and Fox, J. W. 2009. Phase-locking and environmental fluctuations generate synchrony in a predator–prey community. – *Nature* 460: 1007–1010.
- Vité, J. and Williamson, D. 1970. *Thanasimus dubius*: prey perception. – *J. Insect Physiol.* 16: 233–239.
- Volney, W. J. A. and McCullough, D. G. 1994. Jack pine budworm population behaviour in northwestern Wisconsin. – *Can. J. For. Res.* 24: 502–510.
- Weed, A. S. et al. 2016. Data from: Spatio-temporal dynamics of a tree-killing beetle and its predator. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.ms739>>.

- Williams, D. W. and Liebhold, A. M. 2000. Spatial scale and the detection of density dependence in spruce budworm outbreaks in eastern North America. – *Oecologia* 124: 544–552.
- Winder, L. et al. 2001. Modelling the dynamic spatio-temporal response of predators to transient prey patches in the field. – *Ecol. Lett.* 4: 568–576.
- Ydenberg, R. C. 1987. Nomadic predators and geographical synchrony in microtine population cycles. – *Oikos* 50: 270–272.
- Ylloja, T. et al. 2005. Mismatch between herbivore behavior and demographics contributes to scale-dependence of host susceptibility in two pine species. – *For. Sci.* 51: 522–531.
- Zuur, A. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.

Supplementary material (Appendix ECOG-02046 at <www.ecography.org/appendix/ecog-02046>). Appendix 1.