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Are bark beetle outbreaks less synchronous than forest Lepidoptera outbreaks?

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Abstract Comparisons of intraspecific spatial synchrony across multiple epidemic insect species can be useful for generating hypotheses about major determinants of population patterns at larger scales. The present study compares patterns of spatial synchrony in outbreaks of six epidemic bark beetle species in North America and Europe. Spatial synchrony among populations of the Eurasian spruce bark beetle *Ips typographus* was significantly higher than for the other bark beetle species. The spatial synchrony observed in epidemic bark beetles was also compared with previously published patterns of synchrony in outbreaks of defoliating forest Lepidoptera, revealing a marked difference between these two major insect groups. The bark beetles exhibited a generally lower degree of spatial synchrony than the Lepidoptera, possibly because bark beetles are synchronized by different weather variables that are acting on a smaller scale than those affecting the Lepidoptera, or because inherent differences in their dynamics leads to more cyclic oscillations and more synchronous spatial dynamics in the Lepidoptera.

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Introduction

Fluctuations in insect populations have long puzzled ecologists. Early studies searched for “key” mortality agents or density-dependent sources of mortality, while later studies have increasingly been focused on characterizing population behaviour in order to infer the processes that generate that behaviour (Liebhold and Kamata 2000). In particular, the analysis of temporal behaviour through space provides valuable opportunities for understanding why populations fluctuate. Major advances have been made in the theoretical development of how various population processes might interact to produce spatial patterns in the abundance of animal populations (Moran 1953a; Bascompte and Solé 1995; Ranta et al. 1995; Koenig 1999; Peltonen et al. 2002; Johnson et al. 2004; Liebhold et al. 2004).

Spatial synchrony (i.e. synchronous fluctuations over large geographic areas) has been found to be a common feature among insects (Liebhold and Kamata 2000; Peltonen et al. 2002). However, these spatial patterns vary considerably among species and several factors could explain the different dominant patterns (Liebhold et al. 2004). Comparison of patterns of spatio-temporal synchrony in different species may be a useful approach to generate and test hypotheses about causality (Peltonen et al. 2002; Liebhold et al. 2004).

In the present study we have analysed landscape-scale historical outbreak time series for six tree-killing bark beetle species: *Dendroctonus frontalis* Zimmermann (the Southern pine beetle), *D. ponderosae* Hopkins (the mountain pine beetle), *D. pseudotsugae* Hopkins (the Douglas fir beetle), *D. rufipennis* (Kirby) (the North American spruce beetle), *Ips perturbatus* (Eichhoff)(the Northern spruce engraver) and *I. typographus* L. (the Eurasian spruce bark beetle). Ecologically, bark beetles span a continuum from species that can colonize healthy trees to species that are limited to dead wood. Most bark beetles belong to the latter group, but a few species cause major economic impacts due to their habit of killing healthy trees through pheromone-mediated mass attacks (Rudinsky 1962; Beaver 1989). The exact mechanism by which trees are killed is still disputed, but phytopathogenic blue-stain fungi associated with the beetles are probably involved in most cases. However, these phytopathogenic fungi are not sufficient without efficient aggregating pheromones that coordinate beetle mass attacks.

Aggressive bark beetles are some of the most destructive insects in temperate conifer forests and may kill virtually all host trees over extensive areas during outbreaks (Berryman 1982b; Christiansen et al. 1987). For example, *D. ponderosae* killed 80 million pine trees (ca. 30 million m^3) from 1979 to 1983 in the northwestern United States (McGregor 1985). During the same period *D. frontalis* killed pines equivalent to 17.4 million m^3 in the southern states (Hoffard 1985). In Europe, *Ips typographus* has killed around 50 million m^3 of Norway spruce [*Picea abies* (L.) Karst.] in large outbreaks since the late 1940s (Worrell 1983; Christiansen and Bakke 1988; Führer 1996). In addition to these species, *D. rufipennis*, *D. pseudotsugae*, *I. perturbatus* and others kill substantial numbers of trees in North America (Wood 1972; Wood 1982; Wood and Van Sickle 1992; Bright 1976; Furniss and Carolin 1977; Berryman and Ferrell 1988; Holsten and Werner 1997; Werner and Holsten 1997).

Here we have quantified the magnitude and spatial range of synchrony in historical outbreaks of six bark beetle species. The differences and similarities between species were described and compared to characteristics of the study areas and the biology of the individual species to generate hypotheses about what factors are dominating the spatio-temporal outbreak dynamics. Synchrony of bark beetle species was also compared to that of five epidemic forest Lepidopteran defoliators previously analysed by Peltonen and co-authors (2002) to see how major taxonomic groups differ in spatial synchrony.

Materials and methods

Outbreak data

Datasets analyzed in this study were derived from sketch maps of outbreaks for the six bark beetle species (Fig. 1; Worrell 1983). These maps were produced by manually transcribing damaged areas observed from either ground (*I. typographus*) or aerial surveys (other species). These annual outbreak maps describe the distribution of bark-beetle-inflicted tree mortality. Forested areas were defined to be in outbreak status when groups of trees or continuous stands were killed. For *D. pseudotsugae*, *D. frontalis*, *D. ponderosae*, *D. rufipennis* and *I. perturbatus*, outbreak status was determined by one or more spots of killed trees per 1000 acres (~405 ha) of host type (pine or spruce types). Outbreak areas on maps were digitized as polygons and transferred to raster GIS layers [using the Universal Transverse Mercator (UTM) projection] depicting the presence/absence (0/1) of outbreaks in each 1×1 km^2 cell (Williams and Liebhold 2000). The raster cells were subsequently aggregated into 25×25 km^2 and 100×100 km^2 cells for all species except for *D. frontalis*, for which data were only available as outbreak area per county (average county size was about 40×40 km^2). The fraction of original cells that were in outbreak status was used as a proxy for yearly abundance in each aggregate cell. Aggregate cell sizes of 25×25 km^2 were used for comparisons among bark beetles, while comparisons between epidemic bark beetles and forest Lepidoptera were performed using the same cell size that was used in the previous study of Lepidoptera species (100×100 km; Peltonen et al. 2002). Time series for each aggregate cell were obtained by concatenating data from maps in sequential years. Aggregate cells with zero damage over all years were excluded from the analysis.

Analyses of spatial synchrony

Spatial synchrony refers to coincident changes in the abundance or other time-varying characteristics of geographically disjunct populations (Buonaccorsi et al. 2001; Liebhold et al. 2004). Spatial synchrony among several populations can be summarized by plotting pairwise correlations between time series of spatially disjunct subpopulations against the Euclidean distance separating those populations (Liebhold et al. 2004). Generally, populations located near each other tend to be more synchronous than those located farther apart, and the patterns of variation in spatial synchrony with distance differ among species (Ranta et al. 1995; Bjørnstad et al. 1999; Koenig et al. 1999). In the present analyses we used the nonparametric covariance function (NCF) to explore how synchrony decreases with increasing distance (Bjørnstad et al. 1999; Bjørnstad and Falck 2001). The NCF is a smoothing spline function fit to the pairwise cross-correlations as a function of lag distance. Confidence intervals for the estimated functions were calculated using bootstrap resampling of 1,000 iterations (Bjørnstad and Falck 2001). A maximum lag distance of 400 km was selected for the spatial covariance function in order to make the analyses comparable, since this was the smallest dimension among the six datasets (Table 1). Since it was uncertain to what extent differences in time series lengths might affect results, a second comparison of the same species used the mean of the synchrony values based on subdivided non-overlapping time series of 5 years.

The occurrence of at least one outbreak over the time series defined the presence of suitable habitat. Thus a map dataset of suitable habitat was generated for each

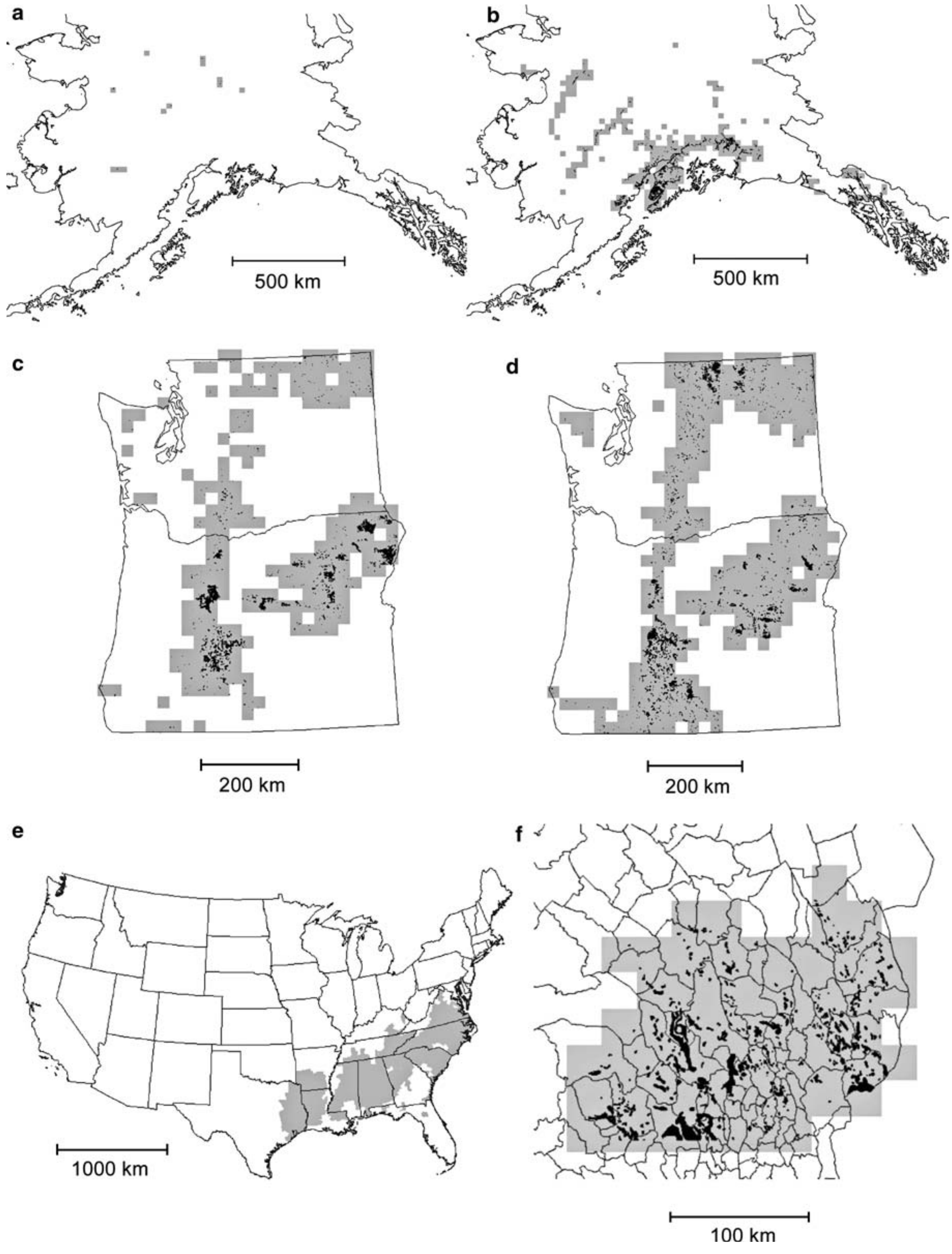

Fig. 1 Maps of historical outbreak areas (see Table 1 for ranges of dates for records) of the bark beetle species studied: (a) Northern spruce engraver—*Ips perturbatus* in Alaska, (b) North American spruce beetle—*Dendroctonus rufipennis* in Alaska, (c) Douglas fir beetle—*Dendroctonus pseudotsugae* in Washington and Oregon, (d) Mountain pine beetle—*Dendroctonus ponderosae* in Washington and Oregon, (e) Southern pine beetle—*Dendroctonus frontalis*, and (f) Eurasian spruce bark beetle—*Ips typographus* in SE Norway

species by recording (0/1) whether there had ever been an outbreak in each cell. Spatial correlograms, that quantified spatial autocorrelation as a function of lag distance, were calculated from habitat datasets for each species (*D. frontalis* was excluded from this analysis because data were only available as outbreak area per

Table 1 Properties of bark beetle species and data sets

Species	Hosts[a]	Generation/yr	Time range[b]	Geographic extent (E-W x N-S, km)	Location[c]
D. frontalis	LP, SP, VP	7–9	1960–1999	1800 × 1400	USA: TX, LA, AL, MS, SC, NC, AR, TN, KY, GA, VA
D. ponderosae	LPP, PP	1	1980–2002	800 × 900	USA: WA, OR
D. pseudotsugae	Douglas-fir	1	1980–2002	600 × 900	USA: WA, OR
D. rufipennis	ES, WS; SS	1[d]	1989–2002	1800 × 1100	USA: AK
I. perturbatus	WS, LS	1	1989–2002	1700 × 1100	USA: AK
I. typographus	Norway spruce	1	1972–1980	400 × 600	Norway

[a] *LP* Loblolly pine; *SP* Shortleaf pine; *VP* Virginia pine; *LPP* Lodgepole pine; *PP* Ponderosa pine; *ES* Engelmann spruce; *WS* White spruce; *SS* Sitka spruce; *LS* Lutz spruce

[b] Time range indicates when the data for each insect species were collected

[c] TX = Texas, LA = Louisiana, AL = Alabama, MS = Mississippi, SC = South Carolina, NC = North Carolina, AR = Arkansas, TN = Tennessee, KY = Kentucky, GA = Georgia, VA = Virginia, AK = Alaska. D = *Dendroctonus* and I = *Ips*

[d] Varies from 1 to 3 yrs

county) using spline correlograms (Bjørnstad and Falck 2001).

Results

In general, the bark beetle species exhibited spatial synchrony over relatively long distances (Fig. 2, Table 2). For all species spatial synchrony was greatest between nearby populations (local synchrony), and spatial correlation declined with increasing lag distance (Fig. 2). There were however considerable differences in the spatial covariance functions among the species. The spatial synchrony of *I. typographus* in Norway was significantly higher than for the five North American bark beetle species at all lag distances (Table 2). The local synchrony was also high for *D. frontalis* (0.74), but the spatial autocorrelation declined more rapidly with distance for the North American bark beetles than for *I. typographus*. The marked difference in synchrony between *I. typographus* and the other species was still apparent when the 5-year time series sequences were used. The mean regional synchrony level of 5-year time series was 0.70 for *I. typographus* and ranged between 0.08 and 0.27 for the other species.

The differences in the spatial correlation functions among the North American bark beetles were relatively small compared to the difference between *I. typographus* and the North American species (Table 2, Fig. 2). Confidence intervals of local synchrony (lag distance = 0) were overlapping for all North American bark beetle species except for *D. frontalis*. Overlapping confidence intervals were also observed among North American bark beetle species at higher lag distances (100–400 km), and in cases where they did not overlap the differences were relatively small and not consistent throughout the range of lag distances (Table 2). The two sympatric species pairs (*D. rufipennis* and *I. perturbatus* in Alaska, and *D. pseudotsugae* and *D. ponderosae* in Washington and Oregon states) exhibited

Fig. 2 The spatial covariance functions (NCF) estimated from outbreak data of six bark beetle species. The upper and lower lines represent the 95% bootstrap confidence intervals

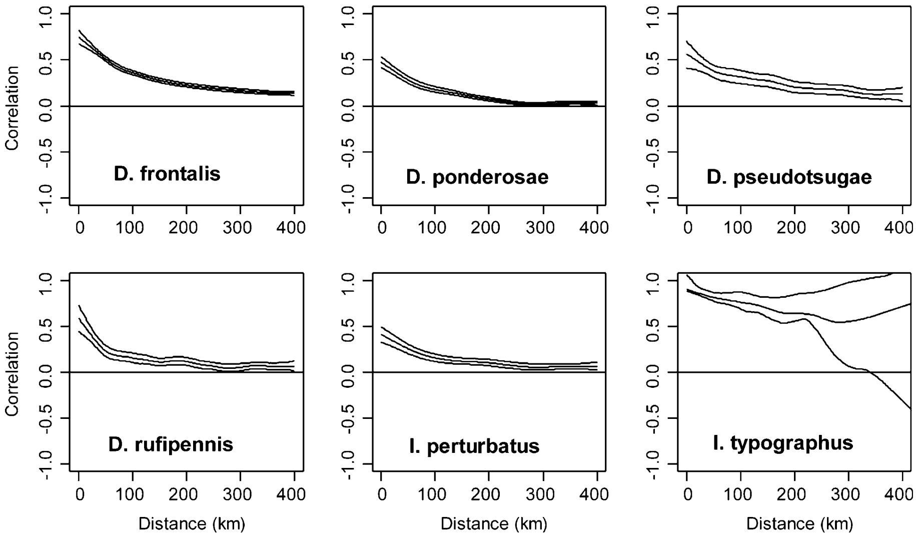

Table 2 Levels of spatial synchrony at five lag distances for outbreaks of six bark beetle species ranked according to the magnitude of local (lag = 0) synchrony. Numbers in square brackets are 95% confidence intervals

Species	Distance (km)				
	0	100	200	300	400
Ips typographus	0.90 [0.88–1.00]	0.76 [0.69–0.87]	0.64 [0.56–0.85]	0.55 [0.07–0.98]	
Dendroctonus frontalis	0.74 [0.67–0.81]	0.36 [0.34–0.38]	0.23 [0.21–0.25]	0.16 [0.14–0.18]	0.13 [0.11–0.16]
Dendroctonus rufipennis	0.58 [0.44–0.71]	0.16[0.11–0.21]	0.12 [0.07–0.16]	0.06 [0.02–0.10]	0.06 [0.01–0.13]
Dendroctonus pseudotsugae	0.56 [0.41–0.70]	0.32 [0.24–0.39]	0.20 [0.15–0.27]	0.16 [0.11–0.21]	0.13 [0.05–0.20]
Dendroctonus ponderosae	0.47 [0.41–0.53]	0.18 [0.15–0.21]	0.07 [0.05–0.09]	0.02 [0.00–0.03]	0.03 [0.01–0.05]
Ips perturbatus	0.41 [0.33–0.49]	0.16 [0.12–0.20]	0.10 [0.07–0.14]	0.06 [0.03–0.09]	0.07 [0.03–0.11]

differences in the shape of synchrony curves (Table 2, Fig. 2). *D. rufipennis* showed a higher local synchrony than *I. perturbatus*, while the spatial synchrony for *D. ponderosae* declined more rapidly with lag distance than for *D. pseudotsugae*.

The contrast in spatial synchrony between *I. typographus* and the other species can also be observed from a visual inspection of the outbreak data. While the outbreak of *I. typographus* occurred over a more or less continuous area, the outbreaks of the other species arose independently in spatially separated sub-areas and did not necessarily spread from a single source. Spatial correlograms of map data indicating the presence/absence of suitable habitat (as judged by at least one year of outbreak) indicated a more continuous habitat for *I. typographus* compared to the other bark beetle species. The local autocorrelation for *I. typographus* habitat was 0.94 (with mean correlation 0.67 in the interval 0–100 km), while similar values for the other species ranged from 0.17 to 0.78 (mean correlation 0.10–0.56 in the interval 0–100 km).

There were striking contrasts in synchrony between the bark beetles presented in the current study and the forest Lepidoptera species analyzed by Peltonen et al. (2002). The bark beetle outbreaks exhibited a generally lower degree of spatial synchrony than the Lepidoptera outbreaks (Willcoxon test of mean difference: $P=0.05$ at 100 km distance and $P=0.01$ at 500 km). Except for *I. typographus*, all bark beetles exhibited lower spatial synchrony than the Lepidoptera at a lag distance of 100 km (Table 3). The spatial synchrony at a distance of 300 km ranged from 0.18 to 0.40 for the Lepidoptera species (mean 0.28), while the spatial synchrony was below this range for all bark beetles except for *I. typographus* and *D. pseudotsugae*. For species that could be compared at the longest lag distances (500 and 700 km), the mean of spatial synchrony was also lower for the bark beetles than for the Lepidoptera species (Table 3).

Discussion

Despite the seemingly ubiquitous presence of spatial synchrony in the dynamics of forest insect populations, the causes of this synchrony are not certain. Three mechanisms are known to cause synchrony: 1) dispersal among populations, 2) synchronized stochastic forcing,

Table 3 Spatial synchrony in outbreaks at different lag distances of six bark beetle species and five forest Lepidoptera species. Spatial synchrony data for the Lepidoptera species are reproduced from Peltonen et al. (2002). Numbers in square brackets are 95% confidence intervals

Species	Distance (km)			
	100	300	500	700
Bark Beetles				
Dendroctonus frontalis	0.36 [0.35–0.38]	0.16 [0.15–0.18]	0.12 [0.10–0.13]	0.06 [0.05, 0.08]
Dendroctonus ponderosae	0.38 [0.25–0.52]	0.15 [0.06–0.24]	0.04 [−0.02–0.12]	
Dendroctonus pseudotsugae	0.41 [0.23–0.60]	0.26 [0.13–0.43]	0.10 [0.02–0.19]	
Dendroctonus rufipennis	0.27 [0.14–0.40]	0.07 [0.00–0.13]	0.02 [−0.03–0.08]	−0.02[−0.07–0.04]
Ips perturbatus	0.39 [0.10–0.73]	0.12 [0.00–0.26]	−0.02 [−0.10–0.07]	−0.03 [−0.11–0.11]
Ips typographus	0.78 [0.28–0.98]	0.47 [0.00–0.88]		
Mean of bark beetles	**0.43**	**0.20**	**0.05**	**0.01**
Forest lepidoptera:				
Choristoneura fumiferana	0.61 [0.56, 0.66]	0.40 [0.35, 0.43]	0.27 [0.23, 0.31]	0.20 [0.15, 0.25]
Choristoneura occidentalis	0.68 [0.50, 0.82]	0.24 [0.06, 0.41]	0.04 [−0.09, 0.23]	
Malacosoma disstria	0.53 [0.35, 0.79]	0.18 [0.00, 0.35]	−0.03 [−08, 0.04]	
Lymantria dispar	0.52 [0.40, 0.64]	0.24 [0.15, 0.34]	0.13 [0.05, 0.24]	0.03 [−0.07, 0.14]
Zeiraphera diniana	0.74 [0.62, 0.82]	0.34 [0.18, 0.50]		
Mean of forest Lepidoptera	**0.62**	**0.28**	**0.10**	**0.12**

often referred to as the "Moran effect," and 3) trophic interactions with other species that are either themselves synchronized or mobile (Liebhold et al. 2004). While it is possible to identify these synchronizing processes in models, identification of the dominant synchronizing processes in field populations is more difficult because all three mechanisms may produce nearly identical signatures of synchrony among populations. The comparisons of patterns of synchrony among different bark beetle species and the comparison of synchrony in Lepidoptera versus synchrony in bark beetle species is intended to provide some clues as to what mechanisms are responsible for synchrony in these populations.

There are few studies of spatial synchrony of bark beetle species (Økland and Bjørnstad 2003). The six species included in the present study are all known to exhibit wide fluctuations in abundance and to have outbreaks extending over large regions. All six species exhibit some form of spatial synchrony in the timing of outbreaks across large geographic areas. Spatial synchrony extending beyond the range of known individual dispersal distances has been found in many insect species (Williams and Liebhold 2000; Peltonen et al. 2002). The most plausible explanation for this phenomenon is the action of random but synchronous changes in population densities caused by (density independent) fluctuations in weather ("Moran effect", Moran 1953b; Royama 1992; Koenig 2002) or resources (Satake et al. 2004). The magnitude of spatial synchrony of *I. typographus* trapping records coincides well with spatial synchrony of climatic variables (Økland and Bjørnstad 2003). Inspection of the datasets analyzed here revealed that many of the bark beetle outbreaks arose independently in spatially separated sub-areas and that there were areas with repeated infestations. Similarly, Peltonen et al. (2002) studying forest Lepidoptera outbreaks also found large-scale spatial synchrony and showed that local dynamics for different outbreak species varied considerably and in a spatially dependent manner.

The North American bark beetles had a much lower level of spatial synchrony than *I. typographus*. Furthermore, the spatial correlation functions declined more rapidly with distance for the North American bark beetles than for *I. typographus*. If the spatial synchrony observed in all of these bark beetles is primarily caused by regional stochasticity, it is possible that the greater synchrony among *I. typographus* populations is a result of a greater synchrony in the stochastic effects on their dynamics. Moran (1953b) showed that the level of synchrony between two populations by linearly density-dependent growth will be identical to the level of correlation in the stochastic component of their dynamics. It is usually assumed that these stochastic effects are the result of the effects of weather on population dynamics, and there is convincing evidence that particular weather characteristics (e.g., July maximum temperature) exhibit similar patterns of synchrony around the world (Koenig 2002). If *I. typographus* population dynamics are more strongly influenced by regionalized weather forcing (i.e., regional stochasticity is large in proportion to local stochasticity in this species) than the other bark beetles, then this could explain, in part, the greater level of synchrony. Indeed, there is evidence that specific types of variability in weather (i.e., major storms resulting in elevated windthrow and increased population growth) plays an essential role in the dynamics of this species (Økland and Bjørnstad 2003).

It is however possible that populations of most of these bark beetle species are primarily synchronized as the result of dispersal among populations. A higher spatial synchrony for *I. typographus* may then reflect the greater degree of habitat connectivity (forests of favourable composition) in southern Norway compared to the areas of the North American species. Indeed the spatial correlograms indicated more homogeneous habitat at least to a range 0–100 km for *I. typographus* compared to the other bark beetle species. If dispersal is a major factor contributing to synchrony in bark beetle populations, then continuous forests could potentially affect population dynamics of *I. typographus* by enhancing interdispersal ("connectivity") between favourable habitats, and thus increasing the spatial synchrony. Consistent with this line of thinking, Johnson et al. (2004) provided evidence for the importance of habitat connectivity in the spatial dynamics of larch budmoth, *Zeiraphera griseana* (Lepidoptera: Tortricidae) outbreaks in the European Alps. They found that synchronous outbreaks occurred among highly connected areas, and that outbreaks tended to move in waves from areas of high connectivity to areas of lower connectivity.

There are several possible explanations for the difference in the level of synchrony between epidemic bark beetles and forest Lepidoptera. First, it is possible that the Lepidoptera are capable of dispersing over greater distances than bark beetles, leading to greater synchrony among Lepidoptera populations. However this seems unlikely since some of the Lepidoptera species studied by Peltonen et al. (2002) were either incapable of dispersal or had very limited dispersal capabilities, yet they exhibited synchrony over longer distances than the bark beetles.

A second possibility is that the weather factors that synchronize these species differ in some fundamental way between the Lepidoptera and the bark beetles. If the weather factors affecting Lepidoptera patterns are synchronous over longer distances than the weather factors affecting bark beetle populations, then this could explain the greater extent of synchrony in the Lepidoptera. Unfortunately, it may be very difficult to determine whether this is indeed the case. Moran (1953b) demonstrated that the importance of a stochastic force may be modest yet cause widespread synchronization of dynamics. Thus, the stochastic weather effects that may be synchronizing the populations studied here may be so small that it would be tricky to identify them. Nevertheless, there is considerable evidence that the dynamics of several bark beetles are strongly influenced by precipitation (e.g., drought) or wind, or a combination of these factors. Bark beetle populations are strongly affected by moisture stress that can diminish tree resistance to attack, and thereby enhance population growth; however, only severe and long-lasting drought stress appears to be of significant importance (Berryman 1982b; Raffa and Berryman 1983; Worrell 1983; Dunn and Lorio 1993; Økland and Berryman 2004). Using spatio-temporal analyses of *I. typographus* populations, Økland and Bjørnstad (2003) found that large windfall events may be a major synchronizer of beetle outbreaks. This strong association with precipitation and wind is generally not as great for forest Lepidoptera, and they may be more heavily influenced by variation in temperature (Koenig et al. 1994; Koenig and Knops 1998; Koenig et al. 1999; Koenig and Knops 2000; Liebhold et al. 2000; Williams and Liebhold 2000). Temperature fluctuations tend to be synchronous over longer distances than precipitation (Koenig 2002) or large windfall events (Økland and Bjørnstad 2003), and this may partially explain why Lepidoptera species exhibit more extended synchrony.

A third possibility is that the difference in synchrony observed between Lepidoptera and bark beetles may be due to differences in the density-dependent processes governing their dynamics. While Moran's original work assumed that populations were governed by linear density dependence, numerous studies have shown that nonlinear processes can greatly affect synchronization (Allen et al. 1993; Grenfell et al. 1998; Ranta et al. 1998; Jansen 1999; Ranta et al. 1999; Bjørnstad 2000; Royama 2005). It has been reported that nonlinear processes that promote population cycles can also promote synchrony, and that the magnitude of the stochastic component affects synchronization (Bjørnstad 2000; Royama 2005). Furthermore, it is well known that trophic interactions with other species may lead to periodic behavior due to time lagged density dependence. However, periodic behavior may also be an indirect effect of processes (e.g., Moran effect or mast seeding) that are acting through the trophical interactions, as exemplified by the oak—*Peromyscus*—Gypsy moth system (Liebhold et al. 2000) or the rowan—apple moth—parasitoid system (Satake et al. 2004). For bark beetles, several studies have emphasized resource-based dynamics that may not result in true periodicity (Berryman 1982a; Berryman 1999; Økland and Berryman 2004; Økland and Bjørnstad unpublished). In general, the time series of Lepidoptera populations tend to be more cyclic than the bark beetle series (Kalkstein 1976; Berryman 1982a; Myers 1988; Berryman 1995; Liebhold et al. 2000; Bjornstad et al. 2002; Turchin 2003; Økland and Berryman 2004), thus the cyclicity-synchrony link may explain the overall differences in levels of synchrony.

While relating the pattern of synchrony of various environmental factors to the pattern of synchrony in population dynamics may be valuable for understanding the role of factors that synchronize local populations, results from spatial analysis of time series data should always be viewed cautiously. Although outbreak maps are good indicators of forest insect populations at high densities, the relationship between infestation level and actual population density is generally nonlinear, thresholded, and subject to considerable variation (Williams et al. 1991; Liebhold et al. 1993; Williams and Liebhold 2000), though the relationship for *I. typographus* appears to be linear (Lindelöw and Schroeder 2000). While there may remain some questions about whether the observed differences in synchrony reflect true differences in population densities or not, our results indicate that there are substantial differences in levels of spatial synchrony among different forest insect taxa.

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