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Synchrony and geographical variation of the spruce bark beetle (*Ips typographus*) during a non-epidemic period

Received: 6 June 2003 / Accepted: 12 September 2003 / Published online: 15 November 2003
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Abstract Spatio-temporal analyses of non-epidemic bark beetle populations may provide insight in dynamics predisposing for outbreaks. The present article presents a spatio-temporal analysis of the population dynamics of *Ips typographus* based on pheromone trap data from southeast and mid-Norway in the post-epidemic period 1979–2002. The analyses include regression analyses, hierarchical cluster analysis, and analysis of spatial synchrony of beetle time series and climatic data by means of nonparametric spatial covariance functions. The mean abundance of beetles declined linearly with latitude. In addition, the time series means were higher in areas with high forest productivity and rocky soils predisposed to drought. The time series patterns differed significantly between northern and southern study areas. The regional synchrony of the time series was fairly high (0.38), indicating that some large-scale climatic factor may influence the dynamics. Windfelling was the external variable showing the most parallel pattern of correlation to the beetle dynamics. We thus posit that large windfall events may be a major instigator and synchronizer of beetle outbreaks in areas subjected to regionalized weather systems.

Keywords Population dynamics · Exogenous forcing · Climatic factors · Windfall

Introduction

Some bark beetle species are notorious tree-killers causing extensive damage in forests of the temperate zone. While most bark beetles depend on dead trees, the aggressive species will, during periods of epidemic outbreaks, switch to killing weakened or healthy trees. A previous model predicts a threshold for active tree killing determined by population size and host tree vigour (Berryman 1978). This assertion is well supported by empirical data (Larsson et al. 1983; Waring and Pitman 1983, 1985; Mulock and Christiansen 1986). The spruce bark beetle, *Ips typographus* L., is considered the most destructive of the bark beetles in the coniferous forests of the Palaearctic region (Christiansen and Bakke 1988). At low population densities this species breeds in newly dead wood of Norway spruce [*Picea abies* (L.) Karst.], while at high population densities it may colonize living trees (Weslien et al. 1989). Periodic outbreaks over the past two centuries have caused catastrophic timber loss in Central and Northern Europe (Annala 1969). The last outbreak (1971–1981) killed the equivalent of 5 million cubic meters of spruce timber within a 140,000 km² area of southeast Norway (Bakke 1989).

Analyses of spatio-temporal patterns of the population sizes during non-epidemic periods may provide insight to the triggers of population outbreaks. Time series have been used to interpret the relative importance of exogenous (density independent) and endogenous (density dependent) factors in several species (Royama 1992; Berryman 1999), including *I. typographus* (Økland and Berryman 2003). Considering the spatial dimension to dynamics can improve our understanding of the governing forces. The scale and the pattern of spatial synchrony can suggest candidate exogenous processes that influence the dynamics of a species. In particular, synchronization over large distances may reflect critical climatic factors operating over large scales (Koenig 2002). Localized dispersal

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may, in contrast, be reflected in synchronization at smaller scales [see however Bjørnstad (2000) for a more detailed discussion]. Furthermore, spatio-temporal patterns may be used to find the characteristic scales of the population dynamics. Even though the various biological processes may cover a whole range of spatial scales (Wiens 1989; Kotliar and Wiens 1990), the dominance of some processes may cause synchrony across scales to be more characteristic for the population dynamics (Bjørnstad et al. 1999b).

The present study analyses the spatio-temporal population dynamics of *I. typographus*. The analyses use a dataset from the systematic pheromone trapping in southeast and mid-Norway in the period 1979–2002. Most of this period was non-endemic (1982–2002), though in mid-1990s the population size is believed to have been just below the epidemic threshold. However, no extensive damage was reported during that period. We conducted analyses to answer the following major questions: (1) How do the mean abundances and patterns of fluctuations vary geographically? (2) Are the population dynamics similar across the whole study area, or do the analyses indicate subdivisions into more local regions? (3) How large areas are spatially synchronized, and how is synchrony a function of distance? (4) What are the similarities in spatial synchrony among beetle populations and climatic factors (windfall, temperature and precipitation)?

The outline of the study is as follows: First the mean abundances of the time series (\bar{N}) are analysed to detect gradients and areas with generally higher or lower population sizes over time. In the second section, variation in time series patterns is analysed using hierarchical cluster analyses. In the third section, the spatio-temporal patterns of beetles and environmental variables are compared by means of nonparametric spatial covariance function.

Materials and methods

Data

The analyses were based on yearly pheromone trapping of bark beetles in the period 1979–2002. On average 512 drainpipe traps baited with synthetic pheromones were deployed each year (Bakke et al. 1983) in 104 municipalities of southeast and mid-Norway (Fig. 1). Trap numbers varied somewhat from year to year, however the relative distribution across districts remained fairly constant. Traps were set out at the end of April in spruce clear-cuts felled the previous winter and the shortest possible distance from sites used in the previous year. Traps were emptied four times until mid August.

Datasets of wind-felled trees, temperature and precipitation were used in the analyses of spatial synchrony. Yearly windfall (m^3) per municipality in the period 1985–2000 was estimated from insurance records documenting insurance claims to the insurance company Skogbrand. The yearly mean of May–July temperatures and precipitation per municipality in the period 1979–2000 were calculated from meteorological datasets developed by EFOKS project (based on all available meteorological stations in the study area). Coordinates of the maps are based on UTM zone 33 within the EUREF89 system (almost the same as the VGS84 system).

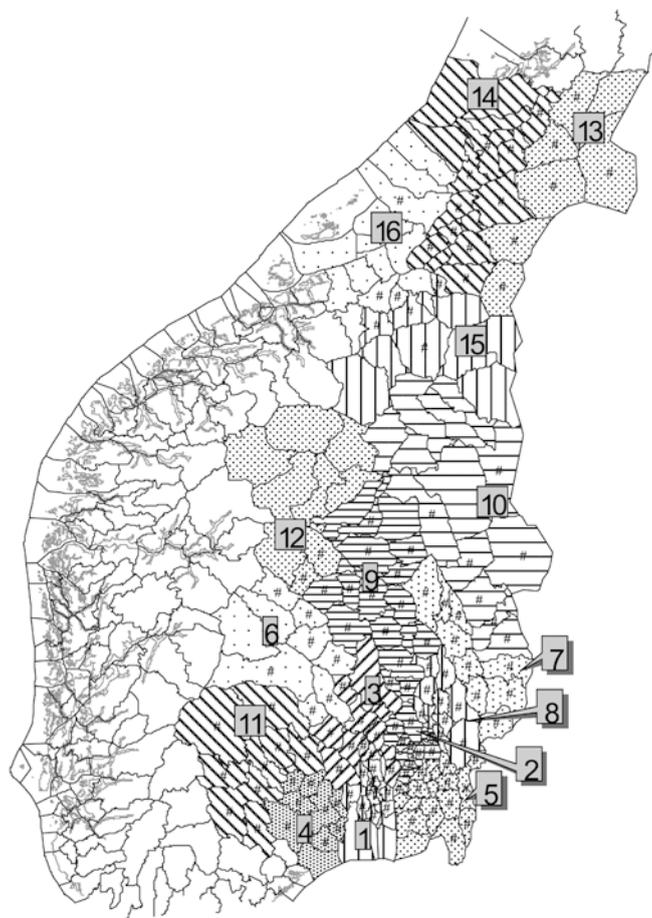


Fig. 1 Map of study area tagged with municipalities (dots) and county parts (numbers) applied in the analyses. Names of county part corresponding to the numbers are given in Fig. 4

Statistical analyses

Population density (N) was expressed as the natural logarithm of the mean number of bark beetles counted per trap per year. A transformation by natural logarithm was applied to weigh down the influence of sites with extreme numbers, and because population growth represents a multiplicative process. The relationship between the abundance and altitude and latitude were tested by multiple linear regression (Rencher 2000). Differences in time series patterns between county parts were analysed by means of hierarchical cluster analyses, using normalized Euclidian distance and single linkage (Rencher 2002). In all regression analyses and cluster analyses, mean population density per trap was calculated for half or whole counties corresponding to the geographical subdivision used by Norwegian entomologists (Fig. 1, average size 6,244 km^2 , range 1,536–14,870 km^2) (Økland 1981).

We applied *ncf*, the nonparametric covariance function (Bjørnstad et al. 1999a; Bjørnstad and Falck 2001), to explore how spatial synchrony in bark beetle dynamics and environmental variables (windfall, temperature, and precipitation) are functions of geographic distance. This method describes how spatial correlation of the various sets of time series depends on the distance separating the sampling locations, and how spatial correlation at shorter distances compares to the regional synchrony within the study area. The *ncf* uses a smoothing spline to estimate the spatial covariance as a function of lag distance (Bjørnstad et al. 1999a; Bjørnstad and Falck 2001). The degree of freedom, which determines the degree of smoothing, was set to the square root of the number of spatial observations (Bjørnstad and Falck 2001). Confidence intervals for

the estimated functions were calculated by means of bootstrap resampling (1,000 iterations). All synchrony analyses were performed on municipality means of parameters and geographical centre points (Fig. 1). Each municipality is on average 659 km² (range: 37–3,178 km²) and harboured on average 5 traps (4–6 traps). In the analysis, we considered the level of regional synchrony, the lag distance at which the correlation between two sites is no greater than the regional synchrony, and the overall shape of the covariance curve. All figures were cut off at two-thirds of the maximum distance between two sites to omit estimation uncertainty in the tail (Isaaks and Srivastava 1989).

All analyses were done in R (<http://www.r-project.org>), except for the cluster analysis that was done in Systat 8.2. The nonparametric covariance function (*ncf*) was calculated using the NCF library available from the authors (<http://onb.ent.psu.edu>).

Results

The mean level of the time series

Latitude was the most important correlate of variation in mean log-abundance (Fig. 2). The abundance decreased significantly with latitude, following the regression

$$y = 21.86(\pm 1.26 \text{ SE}) - 0.0019(\pm 0.0002 \text{ SE})x$$

$$(R^2 = 0.45, P < 0.001) \tag{1}$$

Elevation did not appear as an important determinant of abundance. Adding elevation as a second variable in a multiple linear regression together with latitude did not increase the coefficient of determination.

The mean abundances were particularly low in mid-Norway (circles 13–16 in Fig. 3). The greatest abundances were found at the southern end of the latitudinal gradient. However, the most southern plots at low

altitude included both high and low abundances. Certain areas were distinguished by particularly high abundances (circles 1–4 in Fig. 3).

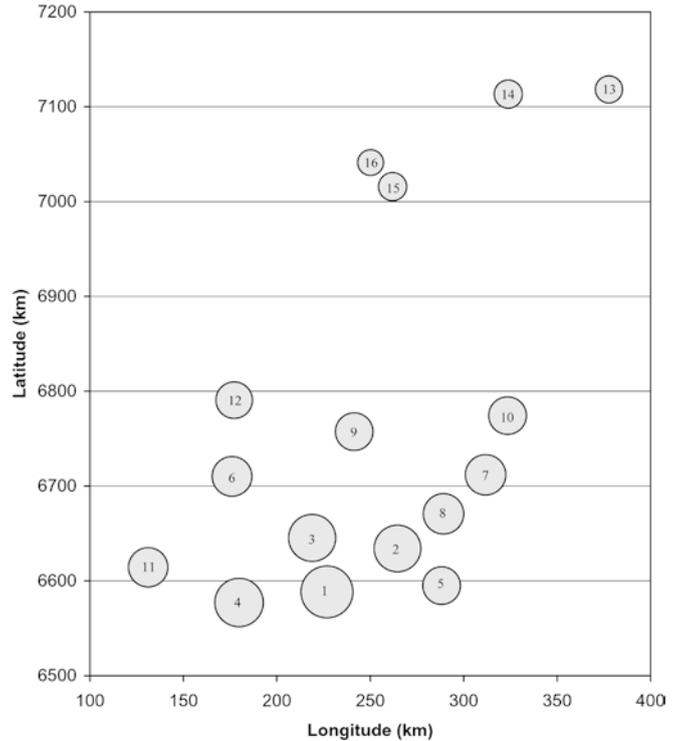
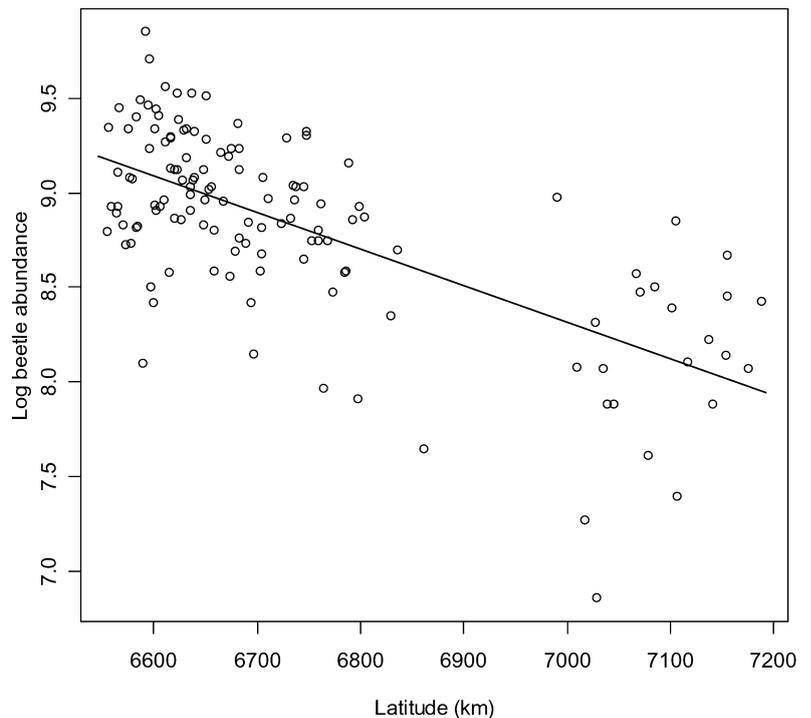


Fig. 3 Geographical bubble plot of beetle abundances (area of circles are proportional with mean of time series) of county part (numbers correspond to county part names given in Fig. 4). Coordinates are based on UTM zone 33 (EUREF89)

Fig. 2 Mean log abundance of *Ips typographus* of municipalities plotted against latitude



Time series patterns

The hierarchical cluster analysis revealed considerable geographical differences in the dynamics of the different regions. The highest degree of similarity was found within the lowland areas of southeast Norway (Fig. 4,

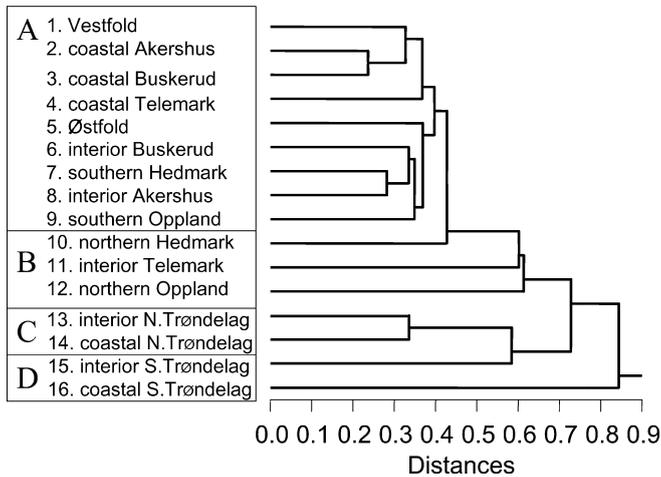
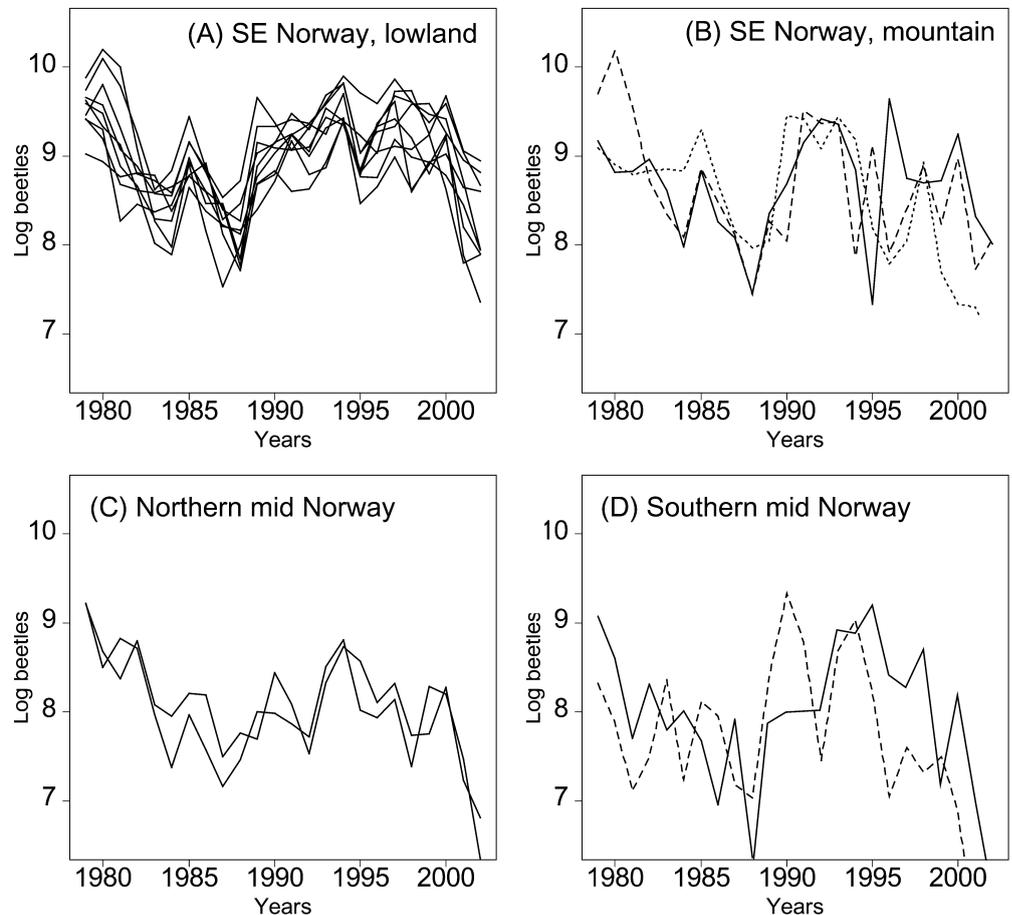


Fig. 4 Hierarchical clustering of time series in county parts (Euclid distance). *A* lowland of southeast Norway, *B* mountainous part of southeast Norway, *C* northern part of mid-Norway, and *D* southern part of mid-Norway

group A) and within the northern part of mid-Norway (Fig. 4, group C), among these all normalized Euclid distances were less than 0.4. The analysis further revealed significant differences between these two areas (Fig. 5). The time series of the lowland areas of southeast Norway (Fig. 5A) show a crude wavy pattern with a “period” of 15 years or more (period is in quotation marks since a cycle can obviously not be concluded from a single wave). Maximum abundances were observed during the beginning of the series (around 1980) and in the middle of the 1990s. The time series of the northern part of mid-Norway (Fig. 5C) show saw-toothed fluctuations around a mean, except for a major drop in the final 2 years. The mean in the northern group is about the same level as the minima of the lowland areas of southeast Norway.

The time series of the mountainous parts of southeast Norway (group B in Fig. 4) cluster closest to the southern lowland time series (A). However they branch off at higher Euclid distances (northern Oppland at 0.61, interior Telemark at 0.60, and northern Hedmark at 0.43) signifying that they are only partially related to the dynamics in the other areas. These time series are more irregular (Fig. 5B), and mix characters from the southern lowland (A) and the northern group (C). For instance the initial abundance of interior Telemark (dashed line in Fig. 5B) was as high as in the southern

Fig. 5A–D Time series plots (log *N*) of county parts corresponding to groups given in Fig. 4 (time series with Euclid distance higher than 0.4 are separated with dashed or dotted lines). **A** Lowland of southeast Norway, **B** mountainous part of southeast Norway (*dashed line* is interior Telemark and *dotted line* is northern Oppland), **C** northern part of mid-Norway, and **D** southern part of mid-Norway (*dashed line* is coastal part of South Trøndelag)



lowlands. Thereafter, however the series exhibit the more irregular fluctuations akin to those seen in mid-Norway. The southern end of mid-Norway block showed the most deviant time series (D in Fig. 4, Fig. 5D). The coastal part of South Trøndelag did not cluster with any other area (Euclid distance of 0.84 to the other areas) (Fig. 4). This time series is also characterized by irregular fluctuations around a mean (dashed line in Fig. 5D) with a wavy pattern well below the average of the lowlands of southeast Norway.

Spatial synchrony

The spatial synchrony of the log abundance size is high across long distances (Fig. 6A). The overall regional synchrony within the study area was 0.38 (95% CI = 0.34–0.42). Populations in close proximity were more synchronized than the regional mean.

The correlation function shows a gradient-like decline with increasing distance in the initial part (Fig. 6A). Starting around 0.50 (95% CI = 0.43–0.58), the function drops to its regional average around 134 km (95% CI = 89.1–218.6 km).

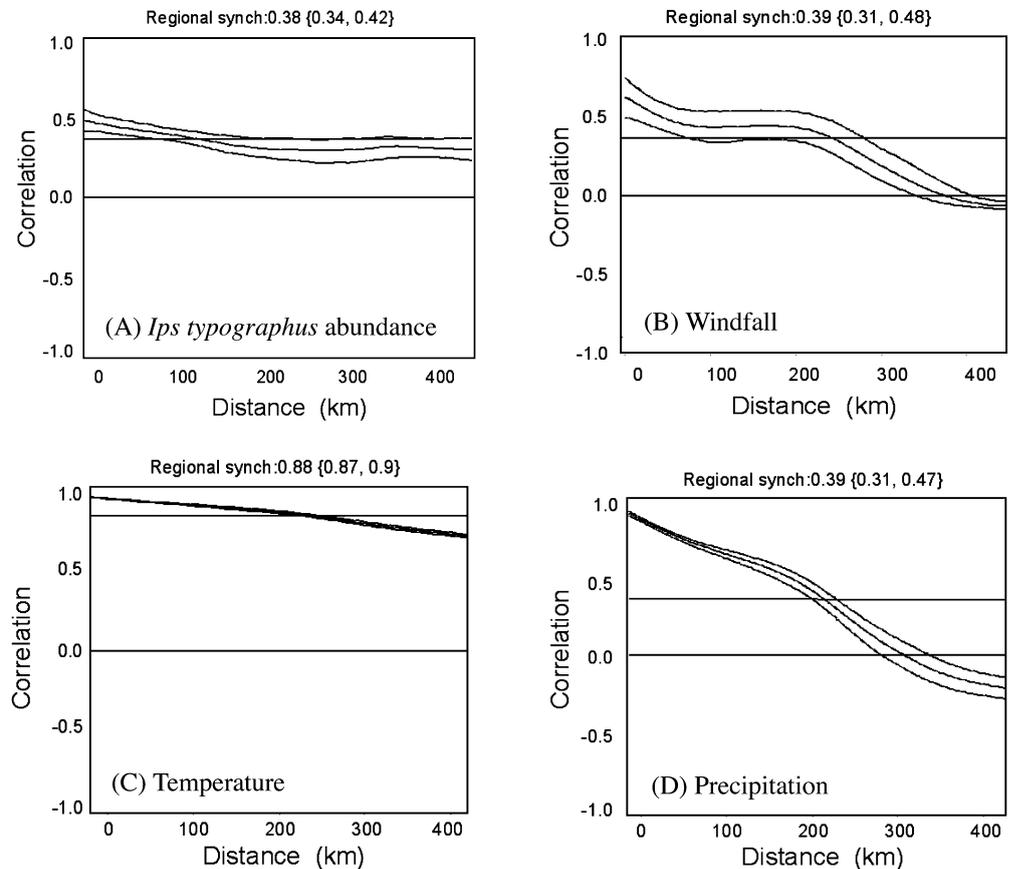
The spatial correlation functions of the environmental variables are presented in Fig. 6B–D. Among these, windfall showed the most similar pattern to that of the bark beetles. For both beetles and windfall (Fig. 6A, B), the correlation is initially just over 0.5, and then falls to

around the level of the regional synchrony. The regional synchrony levels are nearly the same, 0.39 for windfall and 0.38 for beetles. The spatial correlation in windfall tails off at long distances, reaching 0 at about 375 km (Fig. 6B). The initial levels of synchrony are much higher for temperature and precipitation, starting at 1.00 and 0.97 respectively (Fig. 6C, D). The spatial synchrony of temperature remains high within most of the study area, showing a regional level of 0.88 (Fig. 6C). The spatial synchrony of precipitation represents a cline across the study area, reaching 0 at about 323 km (Fig. 6D).

Discussion

Bark beetle abundance decreases with increasing latitude. Latitude is probably best seen as a fudge factor embracing several more direct correlates of population carrying capacity. Winter temperatures have been found to be a limiting factor for the northern distribution of the southern pine beetle (*Dendroctonus frontalis* Zimmermann; Ungerer et al. 1999). However, winter temperatures are believed to be a less important factor for the ground-hibernating *I. typographus* in the present study area (Austarå et al. 1993). Since the southern lowland sites represent both low and high population means, some more area-specific factor is likely to influence the means. Forest productivity decreases with

Fig. 6 Nonparametric spatial covariance function (*ncf*) of beetles and environmental variables. Regional synchrony level with 95% confidence interval (based on 1,000 iterations) is presented above each figure. **A** Log abundance of *I. typographus*, **B** Windfall, **C** Mean temperature of May–July, and **D** Mean precipitation of May–July



latitude and is coupled with the production of host substrates (dead spruce). The areas of largest mean populations appear to embrace the most productive forests. High forest productivity was suggested as a key factor during the *Ips* outbreak of the 1970s (Worrell 1983). In addition, greater drought susceptibility in the thin-soiled, fissured bedrocks, Permian and Precambrian areas were suggested as a factor enhancing damage during this outbreak (Worrell 1983). Severe drought stress weakens the defence of trees against attacks of bark beetles and thereby increases the availability of host substrates (Dunn and Lorio 1993). The largest mean populations of the present study coincide with the Permian and Precambrian areas described by (Worrell 1983).

Within a characteristic spatial scale, some biological processes may be dominant and give more similar population dynamics (Bjørnstad et al. 1999b). It can be deduced from the present analysis that the study area may be subdivided into key areas. Our study indicates a division between southern and northern areas, and between lowland and mountainous areas. However, there is no distinct border between these areas. The dynamics seem to be fairly similar within the lowland of southeast Norway, and within the northern part of mid-Norway. Latitudinal differences in dynamics have also previously been documented in the southern pine beetle in North America (Ungerer et al. 1999).

We believe the differences between southern and northern areas somehow are associated with the mountain ridge subdividing the southern and northern areas. However, dispersal and dispersal constraints are not plausible explanations for this geographical subdivision. Even though *I. typographus* may disperse over long distances (Botterweg 1982; Stenseth 1984; Forsse and Solbreck 1985), the areas of correlation in the present study are too large to be explained by spread of beetle individuals. Dispersal may, however, be one of several locally interacting factors causing the higher correlation at shorter distances.

Wide-scale climatic factors are often implicated to explain the region-wide synchrony in population dynamics (Moran 1953; Royama 1992; Ranta et al. 1995; Koenig 2002; Peltonen et al. 2002). Climate differs in many respects between the northern and the southern areas of the present study area. We focused on three possible climatic drivers in the present study: temperature, precipitation and windfall (and thereby wind). Windfelling was the factor coinciding best with the spatial correlation of beetle dynamics. The regional level of correlation was about the same, and the decay of correlation with distance showed similarities with the beetles for the dominant range of distances (thereafter falling off more rapidly, but this may be linked to secondary edaphic or ecological factors). The spatial synchrony of temperature was fairly high in the whole study area. In this way temperature does not appear to account for the overall pattern of synchrony between the southern and northern areas. The

synchrony curve of precipitation is quite different to that of *I. typographus* in that correlation declines gradually to 0 at around 323 km lag distance. Severe storms are closely coupled with the occurrences of wind felling. This is therefore a plausible factor of population synchronization of *I. typographus*. The importance of windfall episodes in the initiation of *I. typographus* outbreaks has been recognized for centuries (Gmelin 1787; Trägårdh and Butowitsch 1935; Annala and Petäistö 1978; Ravn 1985; Worrell 1983; Gregoire 1988; Schroeder and Lindelöw 2002). Large events of wind felling appear to trigger population increases of *I. typographus* (Worrell 1983; Økland and Berryman 2003). Windfelling is not spatial synchronous between the southern and northern areas (correlation drops to 0 at 375 km), as major wind felling episodes tend to occur at different time in these two regions. The northern area is mainly influenced by the oceanic climate given by the Norwegian Sea to the west of Norway, while the southern area is more often influenced by southern weather systems.

Long-termed climatic changes should be expected to affect the population dynamics of *I. typographus*. For Norway, in particular, climate scenarios predict more frequent and severe storms (Carnell and Mitchell 1996; Kristjansson and Pedersen 1998; Alfsen 2001). Since storm-induced wind felling appears to be a major influence on spruce bark beetle dynamics, an increase in frequency and severity of storms is likely to cause changes in outbreak behaviour in the various regions of Norway. A theoretical model that describes the link between climatic fluctuations and *Ips* dynamics may provide a key vehicle to extrapolate to alternate climatic scenarios of the future.

Acknowledgments This study was performed at the Penn State University, and received financially support from the Norwegian Research Council (the Climate Effect Programme), from Norwegian Forest Research Institute (B.Ø.), and from USDA grant 2002-35302-12656 (O.N.B.). Forest owners and forestry chiefs of the study area are thanked for their contribution to pheromone trap monitoring. The insurance company Skogbrand is thanked for taxation data on wind-felled trees, and EFOKS (Dr. Svein Solberg and co-workers) and DNMI are thanked for providing meteorological data. Dr. Andrew Liebhold (USDA, Morgantown) and Dr. Akiko Satake (Penn State University) are thanked for comments and discussion.

References

- Alfsen KH (2001) Vaeret i 2000: Varmt, vått og vilt. Weather in 2000: warm, wet and wild (in Norwegian). Cicerone 10:5-7
- Annala E (1969) Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). Ann Zool Fenn 6:161-208
- Annala E, Petäistö R-L (1978) Insect attack on windthrown trees after the December 1975 storm in western Finland. Commun Inst For Fenn 94:1-24
- Austarå Ø, Midtgaard F, Saether T (1993) Densities of hibernating *Ips typographus* in the forest litter around attacked and killed spruce trees, with records of spring emergence and flight patterns. Medd Nor Skogforsoeksves 46:1-12

- Bakke A (1989) The recent *Ips typographus* outbreak in Norway—experiences from a control program. *Holarct Ecol* 12:515–519
- Bakke A, Saether T, Kvamme T (1983) Mass trapping of the spruce bark beetle *Ips typographus*. Pheromone and trap technology. *Medd Nor Skogforsøksves* 38:1–35
- Berryman AA (1978) A synoptic model of the lodgepole pine/mountain pine beetle interaction and its potential application in forest management. In: Stark RW (ed) *Theory and practice of mountain pine beetle management in lodgepole pine forests*. USDA Forest Service, Ogden, Utah, pp 95–108
- Berryman AA (1999) Principles of population dynamics and their application. Thornes, Cheltenham, UK
- Bjørnstad ON (2000) Cycles and synchrony: two historical 'experiments' and one experience. *J Anim Ecol* 69:869–873
- Bjørnstad ON, Falck W (2001) Nonparametric spatial covariance functions: estimation and testing. *Environ Ecol Stat* 8:53–70
- Bjørnstad ON, Ims RA, Lambin X (1999a) Spatial population dynamics: analysing patterns and processes of population synchrony. *Trends Ecol Evol* 14:427–431
- Bjørnstad ON, Stenseth NC, Saitoh T (1999b) Synchrony and scaling in dynamics of voles and mice in northern Japan. *Ecology* 80:622–637
- Botterweg PF (1982) Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Z Angew Entomol* 94:466–489
- Carnell S, Mitchell (1996) Assessment of measures of storminess: simulated changes in northern hemisphere winter due to increasing CO₂. *Clim Dyn* 12:467–476
- Christiansen E, Bakke A (1988) The spruce bark beetle of Eurasia. In: Berryman AA (ed) *Dynamics of forest insect populations*. Plenum, New York, pp 479–503
- Dunn JP, Lorio PL (1993) Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L. to *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Environ Entomol* 22:948–957
- Forsse E, Solbreck C (1985) Migration in the bark beetle *Ips typographus* L.: duration, timing and height of flight. *Z Angew Entomol* 100:47–57
- Gmelin JF (1787) *Abhandlung über die Wurmtröcknis*. Cruisiuschen, Leipzig
- Gregoire J-C (1988) The greater European spruce beetle. In: Berryman AA (ed) *Dynamics of forest insect populations*. Plenum, New York, pp 455–478
- Isaaks EH, Srivastava RM (1989) *Applied geostatistics*. Oxford University Press, New York
- Koenig WD (2002) Global patterns of environmental synchrony and the Moran effect. *Ecography* 25:283–288
- Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253–260
- Kristjansson JE, Pedersen K (1998) Varmere klima—flere stormer? *Naturen* 1:18–23
- Larsson S, Oren R, Waring RH, Barrett JW (1983) Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *For Sci* 29:395–402
- Moran PAP (1953) The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Aust J Zool* 1:291–298
- Mulock P, Christiansen E (1986) The threshold of successful attack by *Ips typographus* on *Picea abies*: a field experiment. *For Manage* 14:125–132
- Økland B, Berryman A (2003) Resource dynamic plays a key role in regional fluctuations on the spruce bark beetle *Ips typographus*. *Agr Forest Entomol* (in press)
- Økland KA (1981) Inndeling av Norge til bruk til bruk ved biogeografiske oppgaver/et revidert Strand-system. *Fauna* 34:167–178
- Peltonen M, Liebhold AM, Bjørnstad ON, Williams DW (2002) Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. *Ecology* 83:3120–3129
- Ranta E, Kaitala V, Lindström J, Lindén H (1995) Synchrony in population dynamics. *Proc R Soc Lond Ser B* 262:113–118
- Ravn HP (1985) Expansion of the population of *Ips typographus* (L.) (Coleoptera, Scolytidae) and their local dispersal following gale disaster in Denmark. *Z Angew Entomol* 99:26–33
- Rencher AC (2000) *Linear models in statistics*. Wiley, New York
- Rencher AC (2002) *Methods of multivariate analysis*. Wiley, New York
- Royama T (1992) *Analytical population dynamics*. Chapman & Hall, London
- Schroeder LM, Lindelöw Å (2002) Attacks on living spruce trees by the bark beetle *Ips typographus* (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. *Agric For Entomol* 4:47–56
- Stenseth NC (1984) Observations on dispersal in spruce bark beetles (*Ips typographus* L.). *Fauna Nor Ser B* 31:106
- Trägårdh I, Butovotisch V (1935) Redogörelse för barkborrekampanjen efter stormhärjningarna 1931–1932. *Medd Statens Skogsforskningsinst* 28:1–268
- Ungerer MT, Ayres MP, Lombardero MJ (1999) Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *J Biogeogr* 26:1113–1145
- Waring RH, Pitman GB (1983) Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack. *Z Angew Entomol* 96:265–270
- Waring RH, Pitman GB (1985) Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66:889–897
- Weslien J, et al (1989) Estimating risks for spruce bark beetle [*Ips typographus* (L.)] damage using pheromone-baited traps and trees. *Scand J For Res* 4:87–98
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Worrell R (1983) Damage by the spruce bark beetle in south Norway 1970–80: a survey, and factors affecting its occurrence. *Medd Nor Skogforsøksves* 38:1–34