

Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*

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- Abstract**
- 1 We analysed time series of spruce bark beetles (N_t) caught in pheromone traps from 1979 to 2000 in approximately 100 localities throughout south-east Norway.
 - 2 The analysis was performed at two spatial scales (whole area and 12 sub-regions), and included additional analyses of the time-series sequences before and after a large windfelling (1987) that appeared to induce a shift in the dynamics.
 - 3 Regression of R_t (logarithmic per-capita growth rate) on N_{t-d} indicated that the endogenous dynamics were dominated by lag 1 density dependence. This was particularly so in the sequence after the large windfelling ($R^2 = 0.79$), probably due to intraspecific competition for breeding substrate.
 - 4 The sequence before the windfelling (1979–1987) was declining without significant density dependence. We suggest this to be a transition period, reflecting a drop in carrying capacity due to depletion of susceptible trees during the preceding outbreak period (1970s) and a drop in beetle number to below the density required to kill trees.
 - 5 Windfelling (W_{t-1}) appears to be an important predictor of the dynamics; however, it was difficult to evaluate the statistical significance of this factor due to only one large windfall event.
 - 6 The weak influence of drought stress (D_{t-1}) could be due to the absence of severe drought periods within the time series.

Keywords Climatic factors, density dependence, endogenous feedback, population dynamic, time series.

Introduction

The spruce bark beetle, *Ips typographus* L., is one of the most serious pests of spruce in Eurasia, and periodic outbreaks over the past two centuries have caused catastrophic timber loss in Central and Northern Europe (Annala, 1969). At low population densities, this species breeds in the newly dead wood of Norway spruce (*Picea abies* (L.) Karts.) whereas, at high population densities, it may colonize living trees (Weslien *et al.*, 1989). The last outbreak (1971–1981) killed the equivalent of five million cubic metres of spruce timber within a 140 000 km² area of south-east Norway

(Bakke, 1989). The following period (1982–2002) has been nonendemic, although in the mid-1990s the population size is believed to have been just below the epidemic threshold (Økland & Christiansen, 2002; Økland & Bjørnstad, 2003). The huge losses during the epidemics stimulated accelerated research and, in 1977, the pheromone by which spruce beetles aggregate on and kill their host plant was identified and synthesized (Bakke *et al.*, 1977b). Efforts to control the beetle outbreak led to the widespread use of pheromone-baited traps in Norwegian forests and systematic trapping has been conducted annually since 1979 at approximately 100 sites in south-east Norway to monitor beetle populations and predict outbreaks (Bakke, 1985). A strong linear correlation has been observed between trap captures and tree mortality due to beetle attacks (Weslien *et al.*, 1989; Lindelöw & Schroeder, 2000). Spatio-temporal analysis has

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shown a high degree of synchrony of bark beetle dynamics and climatic variables within south-east Norway (Økland & Bjørnstad, 2003), and previous outbreaks have covered a bigger part of the study area (Worrell, 1983). Even though most of the variables may show some variations at local scale, it is of particular interest to determine the key determinants of the dynamics within the whole area. The aim of the present study was to analyse the trapping data to evaluate the importance of endogenous and exogenous factors as drivers of population fluctuations of the spruce beetle on a large scale.

Methods

Population density (N_t) was expressed as the mean number of bark beetles counted per trap per year over the whole study area of south-east Norway, including the counties Akershus, Buskerud, Hedmark, Oppland, Oslo, Østfold, Vestfold and Telemark. On average, 339 drainpipe traps baited with synthetic pheromones were deployed each year (Bakke *et al.*, 1983). However, because participation is voluntarily, trap numbers have varied somewhat from year to year, although the relative distribution across districts remained fairly constant. Pheromone traps were placed in corners of a 3×3 m square, with the traps of the same model in diagonal corners. 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.

For reasons previously discussed (Royama, 1992; Berryman, 1999), we used the logarithmic per-capita growth rate of the population ($R_t = \ln N_t - \ln N_{t-1}$) as the dependent variable in multiple regression analyses.

Analysis of influential factors was performed on the time series within the whole study area of south-east Norway (approximately 90 000 km²) because spatio-temporal analysis revealed a high similarity of time series and an indication of large-scaled influence of climatic factors within the study area (Økland & Bjørnstad, 2003). Density dependence was also analysed at a smaller scale because this factor may possibly assert an effect at smaller scales. For these analyses, we used the geographical subregions defined by Norwegian entomologists as represented by half and whole counties of average size 6244 km² and range 1536–14870 km² (Økland, 1981). Datasets of the exogenous variables were not available at the subregional level.

A strong windfelling in the autumn 1987 caused a marked increase in abundance of the spruce bark beetle. The importance of windfall episodes in the initiation of *Ips typographus* outbreaks, at least locally, has been recognized by many authors (Gmelin, 1787; Trägårdh & Butovotisch, 1935; Annala & Petäistö, 1978; Worrell, 1983; Ravn, 1985; Gregoire, 1988; Schroeder & Lindelöw, 2002). The possible change in dynamics by the windfelling motivated separate analyses of the periods before (1979–1987) and after (1988–2000) the windfall episode.

Predictor variables were chosen to reflect three conditions:

1. The endogenous feedback structure acting on the beetle population and regulating its dynamics

Feedback processes are usually detected in stationary time series by regressing R_t on N_{t-d} , where d represents the delay, or order, of the feedback response (Royama, 1992; Berryman, 1999). In cases of significant lag 1 density dependence (N_{t-1}), the model of density dependence was tested against a density-independent model (slope = 0) by parametric bootstrap likelihood ratio (PBLR) test (Dennis & Taper, 1994), based on t -values from 10 000 simulated time series of same length and initial value as the original time series.

2. The availability of susceptible breeding substrate

Spruce beetle outbreaks are usually associated with increases in the amount of susceptible host material, particularly wind-thrown trees and trees stressed by drought (Worrell, 1983). We estimated the amount of windfelling after 1985 from insurance records documenting insurance claims for the period 1 October to 30 September. Most windstorms occur between October and March, and trees felled at this time are available for beetle colonization during the following spring and summer. Hence, wind-thrown timber in the current year (W_t) is represented by insurance reports from 1 October of the previous year to 30 September of the current year. Insurance records were not available before 1985. However, written accounts indicate no large wind-fellings before that time. Drought stress (D_t) was estimated by the average of distance (in metres) to the water table during May to July from 14 hydrological stations across south-east Norway.

3. Favourable conditions for beetle flight

Previous studies indicate that 20 °C is a lower threshold for increasing the flight activity of *Ips typographus* (Annala, 1969). The present study used two temperature estimates of favourable weather during the flight period; the number of days that temperatures exceeded 20 °C (the flight threshold) from 1 May to 31 July (T_t), and the sum of temperatures above 20 °C over the same period (S_t). Temperature data were obtained from five meteorological stations representing different parts of south-east Norway (Gardemoen, Kongsberg, Kongsvinger, Lyngdal and Prestbakke). The spatial synchrony of mean summer temperature (May to July) is high within the study area. The nonparametric spatial covariance function (Bjørnstad & Falck, 2001) revealed a regional level of synchrony of 0.92 (Økland, unpublished data).

Results

The time series of population counts (N_t) is shown together with the most important predictors in Fig. 1. Population monitoring using pheromone traps started during the final 2 years of the last outbreak of tree killing. In 1980, the final year of the outbreak, an average of 14 703 beetles were

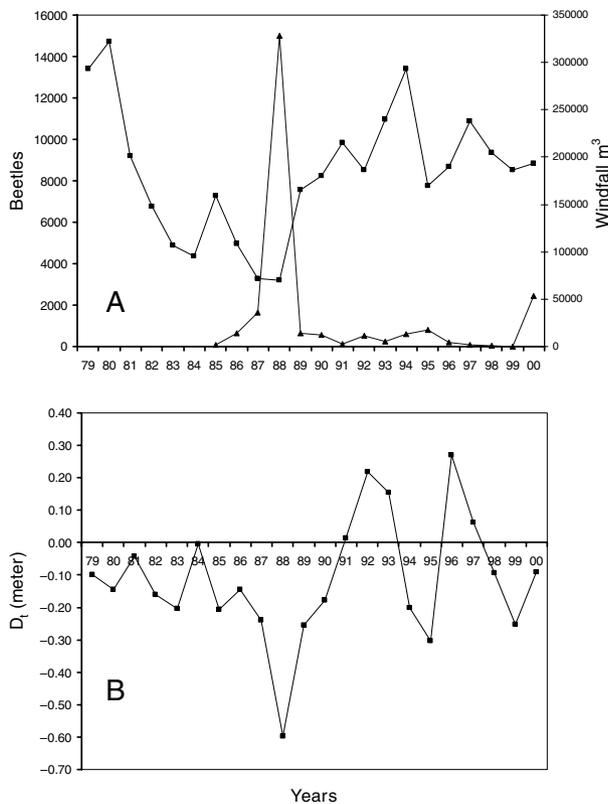


Figure 1 (A) Population density of spruce bark beetles (squares) and amount of windfall (triangles) and (B) deviations from mean depth to groundwater per year in south-east Norway during the period 1979–2000 (windfall data are lacking for 1979–1984).

caught per trap, giving a total catch of almost 4.5 million beetles. In the following years, beetle catches declined steeply until 1988, with a brief upsurge in 1985. Catches then increased for 6 years to a new peak of 13 400 beetles per trap in 1994, or a total catch of 4.2 million beetles. Despite such large captures, no epidemic tree mortality was observed in 1994.

We performed linear regression analysis on the entire time series (1979–2000), with R_t as the dependent variable, N_{t-d} as the endogenous predictor variables, and W_{t-d} , D_{t-d} , T_{t-d} and S_{t-d} as exogenous predictor variables, with d the time delay in the exogenous effect ($d=1$ and $d=2$ were tested). The only significant variable found was initial population size, N_{t-1} , showing a weak influence on the growth rate: $R_t = -4.56 \times 10^{-5} (\pm 2.20 \times 10^{-5}) \times N_{t-1} + 0.36$ ($R^2 = 0.18$, $P < 0.052$). Using a PBLR test, the density-dependent model was found to be close to significant at a 5% level ($P < 0.053$). We analysed the effect of wind-thrown trees (W_{t-1}) only for those years with available data (1985–2000). There was a weakly significant positive relationship between R_t and W_{t-1} , where $R_t = 2.81 \times 10^{-6} (\pm 2.20 \times 10^{-5}) \times W_{t-1} - 7.39 \times 10^{-2}$ ($R^2 = 0.43$, $P < 0.005$).

A tremendous windfelling took place over most of the study area in the autumn 1987, which is shown as year 1988

in Fig. 1(B) because the insurance year used as basis for the data runs from 1 October to 30 September. This large input of breeding substrates was followed by the largest yearly increase of the population between the years 1988 and 1989 ($R = 0.86$) and, subsequently, fluctuations around a relatively constant mean level suggesting an increase in carrying capacity (Fig. 1A). A possible shift in the dynamics due to this large windfall event motivated a separate examination of the time series before (1979–1987) and after the wind-felling (1988–2000).

Regression analysis was performed on both sequences in the same way as for the entire time series. In the first sequence (1979–1987), there was no significant influence of the initial population size or exogenous variables. Wind-thrown trees, W_{t-1} , could not be included in this analysis due to absence of data; however, written accounts indicate no large windfall episodes in this period. In the second sequence (1988–2000), the initial year (N_{t-1}) was the most significant predictor, and with an even more clear influence than on the whole time series ($R^2 = 0.79$) (Table 1). A PBLR test revealed that the density dependence was significantly different from a density-independent null model ($P < 0.0001$). The partial rate correlation function (Berryman & Turchin, 2001) indicated that 78% of the variation in R -values was associated with captures in the initial year (N_{t-1}) whereas no lag 2 density dependence (N_{t-2}) was found. Windfall (W_{t-1}) was a competing predictor in simple regressions, but with lower coefficient of determination than initial population size ($R^2 = 0.54$). However, excluding the years 1988 and 1989 from the analysis showed that wind-felling after this time explained less than 1% of the variation in R -values, and indicated that the main effect was due to the large windfall in 1987/1988. All other exogenous variables had very low coefficients of determination in simple regression ($R^2 < 0.1$). However, in two-variable multiple regression, drought stress (D_{t-1}) produced a weak influence when combined with initial population size ($R^2 = 0.91$). The best three-variable multiple regression included N_{t-1} , D_{t-1} and W_{t-1} ($R^2 = 0.85$). The addition of drought stress in the previous year (D_{t-2}) improved resolution to 0.92. Temperature data contributed very little to the variability in beetle rates of increase.

Regression analysis of the lag 1 density dependence was repeated at a smaller spatial scale to see if the result would differ from those achieved by using the whole study area. We used the geographical subregions defined by Norwegian entomologists. However, the degree of density dependence was found to be about the same level as for the whole study area (Table 2). Using the whole series (1979–2000), the density dependence was significant in all subregions except for two areas (northern Oppland and coastal Telemark), but the influence was fairly low (R^2 ranging from 0.20 to 0.36) (Table 2). In the first sequence (1979–1987), no subregions showed significant density dependence (P -values ranged between 0.11 and 0.51). By contrast, the density dependence was clearly significant from 1988 to 2000 in all subregions except for northern Oppland, with R^2 ranging from 0.45 to 0.79 (Table 2).

Table 1 Simple and multiple linear regressions of exogenous and endogenous variables on per-capita growth rate

	Coefficient	SE	<i>t</i>	<i>P</i> -value	<i>F</i>	Sign. of <i>F</i>	<i>r</i> ²	Adjusted <i>r</i> ²
Best single predictor:								
Intercept	1.156	1.80×10^{-1}	6.41	0.00008				
N_{t-1}	-0.00012	1.96×10^{-5}	-6.15	0.0001	37.76	0.0001	0.79	
The best combination of two predictors:								
Intercept	1.383	0.201	6.88	0.00007				
N_{t-1}	-0.00014	2.1×10^{-5}	-6.80	0.00008				
D_{t-1}	-0.38138	0.2023	-1.89	0.09	25.48	0.0002	0.85	0.82
The best combination of three predictors:								
Intercept	1.085	0.211	5.14	0.0009				
N_{t-1}	-0.00011	2.2×10^{-5}	-5.17	0.0009				
D_{t-1}	0.563	0.18502	3.04	0.016				
W_{t-1}	1.4×10^{-6}	6.3×10^{-7}	2.28	0.052	26.67	0.0002	0.91	0.88

Discussion

Our analysis suggests that competition for host substrate is the main factor regulating populations of *Ips typographus*. Lag 1 density dependence, as observed both at small and large scales, is typical for populations constrained by intra-specific competition for breeding substrates (Berryman, 1999). Intra-specific competition is also indicated by previous studies of sister brooding (i.e. beetles tend to leave crowded logs to find new breeding substrates) (Martinek, 1956; Yumaguchi & Koizumi, 1967; Annala, 1969; Bakke *et al.*, 1977a) and experiments showing decreasing breeding

success with increasing density of *I. typographus* (Thalenhorst, 1958; Ogibin, 1973; Anderbrant *et al.*, 1985). Furthermore, competition for breeding substrates is important in regulating populations of other bark beetle species (Berryman & Pienaar, 1973; Coulson *et al.*, 1976; Raffa & Berryman, 1983).

However, there is a remarkable difference in density dependence between the two time-series sequences. We believe the difference can be explained by the two substrate types setting the carrying capacity of *I. typographus*: (i) susceptible trees that can be killed when the beetles are numerous enough and (ii) recently dead wood such as

Table 2 Simple linear regression of growth rate (*r*) on initial population size (N_{t-1}) in subregions presented by slope, significance (*P*), coefficient of determination (*r*²) and *P*-value of parametric bootstrap likelihood ratio (PBLR)-test of density dependence

Subregions	Slope (\pm SE)	<i>P</i> _{slope}	<i>r</i> ²	<i>P</i> _{PBLR}
Entire time series (1979–2000):				
Østfold	-8.65×10^{-5} ($\pm 3.00 \times 10^{-5}$)	0.01	0.30	0.01
Coastal Akershus	-4.61×10^{-5} ($\pm 1.99 \times 10^{-5}$)	0.03	0.22	0.03
Interior Akershus	-6.91×10^{-5} ($\pm 3.00 \times 10^{-5}$)	0.03	0.23	0.03
Southern Hedmark	-5.34×10^{-5} ($\pm 2.33 \times 10^{-5}$)	0.03	0.22	0.03
Northern Hedmark	-1.21×10^{-4} ($\pm 4.37 \times 10^{-5}$)	0.01	0.29	0.01
Southern Oppland	-1.02×10^{-4} ($\pm 3.53 \times 10^{-5}$)	0.01	0.30	0.01
Northern Oppland	-6.36×10^{-5} ($\pm 3.57 \times 10^{-5}$)	0.09	0.14	0.09
Coastal Buskerud	-4.02×10^{-5} ($\pm 1.79 \times 10^{-5}$)	0.04	0.21	0.04
Interior Buskerud	-6.99×10^{-5} ($\pm 2.12 \times 10^{-5}$)	0.004	0.36	0.003
Vestfold	-3.47×10^{-5} ($\pm 1.61 \times 10^{-5}$)	0.04	0.20	0.04
Coastal Telemark	-3.03×10^{-5} ($\pm 1.78 \times 10^{-5}$)	0.10	0.13	0.11
Interior Telemark	-5.80×10^{-5} ($\pm 2.65 \times 10^{-5}$)	0.04	0.20	0.04
Sequence after windfall (1988–2000):				
Østfold	-1.26×10^{-4} ($\pm 3.00 \times 10^{-5}$)	0.002	0.64	0.002
Coastal Akershus	-1.06×10^{-4} ($\pm 1.71 \times 10^{-5}$)	0.001	0.79	0.0002
Interior Akershus	-1.69×10^{-4} ($\pm 3.00 \times 10^{-5}$)	0.001	0.76	0.0001
Southern Hedmark	-1.11×10^{-4} ($\pm 2.13 \times 10^{-5}$)	0.001	0.73	0.0006
Northern Hedmark	-1.51×10^{-4} ($\pm 5.34 \times 10^{-5}$)	0.02	0.45	0.02
Southern Oppland	-1.34×10^{-4} ($\pm 3.15 \times 10^{-5}$)	0.002	0.64	0.002
Northern Oppland	-6.59×10^{-5} ($\pm 4.94 \times 10^{-5}$)	0.21	0.15	0.21
Coastal Buskerud	-7.40×10^{-5} ($\pm 1.72 \times 10^{-5}$)	0.002	0.65	0.003
Interior Buskerud	-1.10×10^{-4} ($\pm 2.85 \times 10^{-5}$)	0.003	0.60	0.004
Vestfold	-6.71×10^{-5} ($\pm 1.97 \times 10^{-5}$)	0.007	0.54	0.007
Coastal Telemark	-9.04×10^{-5} ($\pm 2.12 \times 10^{-5}$)	0.002	0.65	0.001
Interior Telemark	-1.57×10^{-4} ($\pm 4.91 \times 10^{-5}$)	0.01	0.51	0.008

wind-felled trees (Christiansen *et al.*, 1988). The large outbreak in the 1970s (Bakke, 1989) preceding the first time-series sequence (1979–1987) had presumably depleted most of the trees susceptible to beetle attacks. Absence of significant windfall events, and a population declining below the threshold that is necessary for killing susceptible trees (Berryman, 1982), should result in a continuous population decline, as observed in the first time-series sequence. Density dependence would not easily be detected during this transition because conventional tests require stationary dynamics (Turchin *et al.*, 1995). In the second sequence (1988–2000), a large windfelling increased the population rapidly to a level capable of killing susceptible trees. Subsequently, the beetle population fluctuated with high frequency around a new carrying capacity, presumably set by the availability of both windfall and susceptible trees. This latter portion of the time series shows a marked saw-toothed pattern of fluctuation and a strong negative correlation between R_t and N_{t-1} .

Windfelling (W_{t-1}) is probably an important driver for the dynamic of *I. typographus* on a large scale. In the analysis of spatial correlation, windfelling was the external variable most highly correlated to the beetle dynamics, suggesting that large windfall events may be a major instigator and synchronizer of *I. typographus* outbreaks in areas subjected to regionalized weather systems (Økland & Bjørnstad, 2003). In the current analysis, the large windfelling of 1987 appeared to induce a large-scale shift in the dynamics. However, it is hard to evaluate the statistical significance of windfelling in regression analysis because there was only one large windfall event within the study area during the time series.

Even though the population size in 1994 (the maximum reached after the big windfall) was nearly the same as in the most recent outbreak years (1979 and 1980), no new outbreak of tree killing was started. This might indicate that the risk of outbreak is not only set by the population size, but also severe and long-lasting drought stress may be important for the start of outbreaks by making more trees susceptible to beetle attacks (Berryman, 1982; Worrell, 1983). For example, the two previous epidemics in Norway (in the 1850s and 1970s) were both preceded by long periods of severe drought (Worrell, 1983). However, some studies indicate that whereas severe drought increases the risk of attack, moderate drought may even make the spruces more resistant against beetle attacks (Dunn & Lorio, 1993). The absence of severe drought in the present time series might explain the minor influence of drought in the regression analysis, and also why no new outbreak started during the year of large population (1994).

There are several indications that climatic changes could have important effects on the spruce forests of Scandinavia. Powerful windstorms and extended periods of severe drought appear to be important triggers for *I. typographus* outbreaks. Hence, long-term climatic changes, such as global warming, which may cause an increased incidence and severity of winter storms and summer droughts, could greatly affect the population dynamics of this species, and lead to serious consequences for forestry.

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