

Site condition and predation influence a bark beetle's success: a spatially realistic approach

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- Abstract**
- 1 Spatial pattern in abundance of *Dendroctonus micans* was studied in a 600-ha spruce stand in the Massif Central (Lozère, France). The proportion of trees attacked was measured in 38 plots and these data were used to estimate spatial pattern of attack density in the stand and to identify a transect of decreasing attack density (80% to 30%) over less than 1000 m.
 - 2 Spatial variation in attack density was analysed in relation to (i) data on site and stand characteristics (altitude, slope, tree density, tree average height, yield class and average age) collected from 63 points in the stand and (ii) the releases of the predator *Rhizophagus grandis* (localization and number of beetles released).
 - 3 The proportion of attacked trees was analysed using geostatistics and showed a strong spatial structure reflecting the spatial scale of interaction of *D. micans* with its environment. The spatial structure was modelled in order to estimate the spatial distribution of attack density at unsampled locations.
 - 4 A linear model relating interpolated attack density to the number of predators released 6–10 years before the survey in a 300-m radius and to the average slope over a 250-m radius explained 67% of the observed variability. Spatial autocorrelation was taken into account in a spatial regression model.

Keywords Biological control, *Dendroctonus micans*, geostatistics, insect/host-tree relationships, *Rhizophagus grandis*, spatial ecology.

Introduction

If damage caused by insect pests was always spatially homogeneous, the impact could be measured in a small part of the crop and the observed damage extrapolated to the entire field or forest stand. This is rarely the case and pest populations often exhibit various degrees of patchiness. The extent of spatial variation in abundance and damage is directly related to the number of samples that must be taken to obtain reliable estimates. Spatial patterns of insect pest populations are thus critical from a pest management perspective. The analysis of spatial patterns in pest abundance can be a valuable method to explore spatial relationship between a pest and its habitat. Even if spatial patterns may appear difficult to interpret because several different processes, such as dispersal, reproduction and mortality, may generate the same pattern, their study is often of

great help in rejecting or validating hypotheses on ecological processes, and many ecologists acknowledge the importance of studying spatial components of ecosystems (Kareiva, 1994). Recent developments in theoretical ecology (Tilman & Kareiva, 1997) and landscape ecology (Turner, 1989; Gustafson, 1998) have supported the emergence of spatially explicit analyses and models that bridge the gap between spatial pattern descriptions and analysis of ecological processes (Jonhson, 1989; Zhou & Liebhold, 1995; Coulson *et al.*, 1996; Roland & Taylor, 1997; Sharov *et al.*, 1997). The development of analytical methods such as geostatistics (Rossi *et al.*, 1992; Cressie, 1981; Isaaks & Srivastava, 1989; Deutsch & Journel, 1992) and of utilities such as geographical information systems (GIS) (Burrough, 1986; Liebhold *et al.*, 1991) have greatly contributed to this emergence. Here, we describe spatial variation in density of a bark beetle population in a 600-ha forest stand and attempt to identify the processes and environmental features responsible for this variation.

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Dendroctonus micans (Kugelann) (Coleoptera, Scolytidae) is a pest of apparently healthy spruce trees (*Picea* spp.) in Eurasia. This insect has unique characteristics which result in dispersal patterns quite different from those of other primary bark beetle species. Sib-mating is a common rule: nearly 90% of females emerge from their brood system already fertilized (Vouland *et al.*, 1984), and male beetles do not join females in their new galleries. Tolerance to spruce chemical defenses is extremely high (Everaerts *et al.*, 1988), and successful establishment does not depend on mass-attack or tree mortality (Grégoire, 1988) as in other primary bark beetles (Wood, 1982). Each single female is thus capable of creating a new colony wherever she migrates. Dispersal and establishment are regulated by movements of individual females and by host resistance, and are independent of pheromone perception (the adults do not produce aggregation pheromones), of population thresholds (there is no need for mass-attack of the host trees), and of finding a mate. The long-distance dispersal of *D. micans* in Europe has probably been facilitated by timber transportation, whereas direct flight allowed stand-to-stand and within-stand dispersal (a good example of stratified dispersal, as defined by Hengeveld, 1989). *D. micans* causes significant damage at the range of its geographical distribution, which has considerably expanded in Europe over the last 100 years. The population dynamics of the insect at this scale are marked by the following successive events: invasion of an uncolonized areas, population outbreaks and stabilization of the population at an endemic level (Grégoire, 1988). The specific predator *Rhizophagus grandis* Gyll. (Grégoire *et al.*, 1989), which has simultaneously expanded its range along with *D. micans* from Siberia, is thought to be the main cause of the pest population decrease. However, this regulation is delayed, which is attributed to the lower dispersal abilities of *R. grandis* in following its prey under natural conditions [200 m per year (Grégoire *et al.*, 1985; Fielding *et al.*, 1991; Van averbeke & Grégoire, 1995) compared to an assumed dispersal ability of 1–10 km per year in *D. micans* (Forsse, 1989)], and to the fact that *D. micans* may take advantage of timber shipments over long distances and natural barriers to establish in areas not likely to be naturally reached by its predator (e.g. the UK, Bevan & King, 1983). Even when it is artificially introduced as part of a biological control strategy, unpublished observations indicate that *R. grandis* requires several years of population growth following establishment before it has a significant impact on its prey population.

Because dispersal is independent of pheromone perception, studies on the dispersal of *D. micans* cannot rely on mark–recapture experiments using pheromone traps. However, the attacked trees usually remain alive for years, allowing spatial analyses based on periodic field censuses. Using such data, one study by Gøhrn *et al.* (1954) provided cartographic data on infestation changes over time in one stand. On a much larger scale, Fielding *et al.* (1991a) provide a description of the spread of *D. micans* in the UK between 1982 and 1989; Dolmans & Grégoire (1992) describe the use of a GIS database for *D. micans* population management in

the Massif Central (France). However, none of these studies attempted to relate spatial patterns observed in *D. micans* with other environmental features. In a former study, we analysed the spatial relationship of *D. micans* to the host-tree in small plots of approximately 200 trees and, among other things, demonstrated that its flight range greatly exceeded plot size (Gilbert *et al.*, 2001). The present work addresses a wider scale (2–3 km), closer to the assumed flight range and yet small enough for detailed observations, presenting more environmental spatial heterogeneity than the smaller plots previously analysed. We chose to relate variations in population densities at the scale of this study to environmental factors such as site and stand conditions (altitude, slope, soil quality, trees density, trees average height, yield class and average age), which may affect the resistance of trees and therefore beetle establishment, and to the possible impact of earlier releases of the specific predator, *R. grandis*. Establishing such an association would be important for optimization of silvicultural practices and predator releases, and for improving the understanding of the processes involved in beetle dispersal and establishment.

Materials and methods

Data

Data were collected in 1996, 1997 and 1998 in a heavily attacked spruce stand in the State forest of 'La Croix-de-Bor' (44°44'-N, 03°33'-E, Massif Central, Lozère, France). On average, trees were 60 years old, average stand density was 770 stems/ha and elevation ranged from 1360 to 1500 m. The soil was composed of cryptopodzolic rankers resting on porphyroid granite (Ph. Durant, Office National des Forêts de la Lozère, personal communication). The nearby surrounding land cover was mainly (75%) open fields and the remainder consisted of patches of spruce connected to the study stand.

In the summer of 1996, the proportion of trees attacked by *D. micans* was measured in 38 subplots (Fig. 1). The estimate was based on visual examination of all trees (at least 60) at each subplot (average size 800 m²). Trees were recorded as having been attacked when they exhibited fresh signs of current year boring activity (resin tubes, frass, saw dust). Initial data indicated the existence of a gradient of decreasing attack intensity, ranging from 30% to 80% over less than 1000 m (Fig. 1). The locations of subplots were chosen randomly, except along the transect where additional subplots were surveyed.

Air temperature was measured at hourly intervals during the 1997 growing season using five data loggers (Optic Stowaway temperature logger, Ouset Computer Corporation, Pocasset) installed every 200 m along the transect previously described. These measurements were made in order to determine if microclimatic variations could be observed along the transect. In 1998, analyses of soil texture, water loss and organic matter were performed on soil samples taken at 50-m intervals along the transect at three different depths (10 cm, 30 cm, 50 cm). Water loss was estimated using weights of fresh and dried samples. Particle size

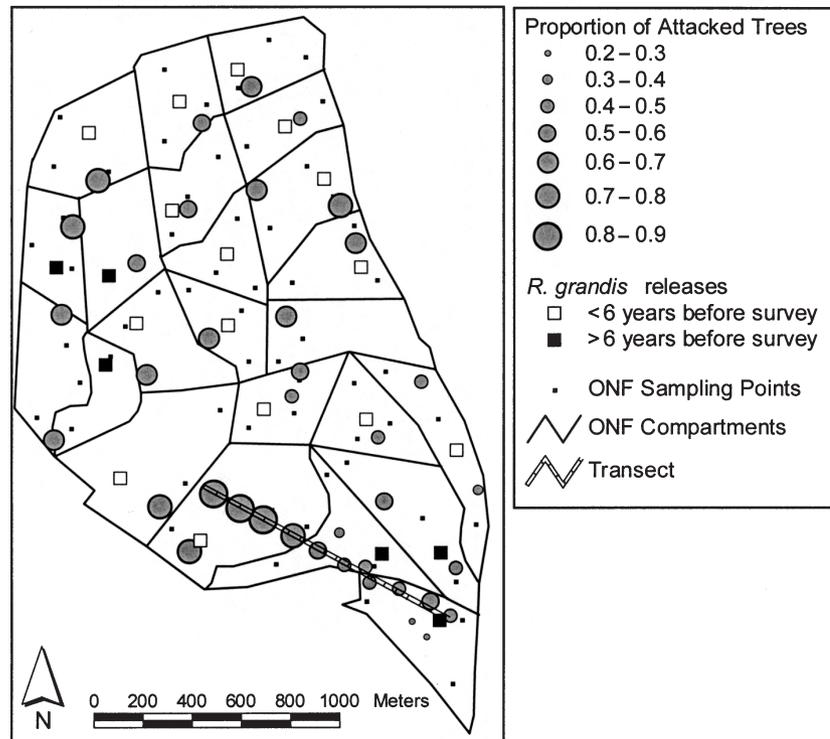


Figure 1 Map of sampling points: attack intensity assessments, 'Office National des Forêts' (ONF, France) site and stand parameters sampling locations, locations of *Rhizophagus grandis* release, ONF compartments (management units) and location of the transect.

distribution was determined using the pipette method after H_2O_2 pretreatment and Na-polyphosphate dispersion. Organic matter was analysed by dry combustion (Strohlein analysis).

In 1997 and 1998, Office National des Forêts (ONF, France) personnel recorded a series of site and stand parameters (altitude, slope, trees average height, yield class and average age) at 63 points located throughout the study area (Fig. 1). ONF also provided historical records of all *R. grandis* releases (location and number of beetles) carried out in the study area (Fig. 1). *D. micans* was first observed in the study area in the late 1970s and the first attempts of biological control by *R. grandis* started in 1988. These releases were made in locations where *D. micans* population density was thought to be the highest at the time of releases. In total, 35000 *R. grandis* individuals were released in the study area during 1988–1996. Unpublished observations of the impact of *R. grandis* releases on *D. micans* populations reveal that 6–8 years are required before the host population starts to significantly decrease, especially if population density is high at the time of the first releases. Establishing a link between attack density and predator releases may thus be difficult when using pooled historical data because recent releases which had no time to establish cannot be differentiated from older ones. It was thus decided to extract a subset of 'old releases' (>6 years before survey) from these historical records, which potentially may have led to predator establishment and impact on *D. micans* population.

Geographical coordinates (XY and elevation) of all sampling points were estimated in the field using a GPS

(GeoExplorer II, Trimble, Sunnyvale) and postprocessing differential correction. All data and collection points were integrated into a GIS database (ArcView GIS 3.0, ESRI, Redlands) for further analysis and modelling.

Analysis

The spatial dependence of the transformed [$\arcsin(x)$] percentages of attacked trees (further referred to as 'attack intensity') were studied using geostatistical techniques. These tools allow exploration and quantification of the spatial autocorrelation, which is the tendency of points close to each other to have more similar values than points farther apart (Isaaks & Srivastava, 1989; Rossi *et al.*, 1992; Cressie, 1993). There are different tools in geostatistics to explore and quantify the spatial continuity of a data set. The most useful are *h*-scatterplots, semivariograms, non-ergodic correlograms and non-ergodic covariance measures (Rossi *et al.*, 1992). The semivariogram is the most common of these estimators: let x_i be an observation at location i and x_{i+h} an observation at lag h (h can be a scalar or a vector), the estimator of the semivariance at lag h is given as (Rossi *et al.*, 1992):

$$\hat{\gamma}(h) = \frac{\sum_{i=1}^{N(h)} (x_i - x_{i+h})^2}{2N(h)}$$

where $N(h)$ is the number of data points separated by a spatial lag of h (Pannatier, 1996). In the presence of spatial dependence, the semivariogram is typically small at small

lags, and increases when the lag increases. In most cases, there is a lag value beyond which the semivariogram estimator no longer increases (spatial dependence is no longer perceptible): this lag value is called the range, and the corresponding semivariogram plateau is known as the sill. The most widely used geostatistical techniques assume that the random process is stationary (i.e. that neither the expectation of the process nor their variogram are dependent on location). In stationary processes, and when the study-area radius is large as compared to the range, the sill value is equal to the process variance. For comparison purpose, the non-ergodic correlogram ($1 - \rho(h)$) was also used to estimate the semivariance for its ability to filter local mean and variance (Rossi *et al.*, 1992).

The semivariogram and the non-ergodic correlogram of attack intensity were calculated using the software VARIOWIN (Pannatier, 1996). Semi-variogram estimates made at distance classes higher than 1250 m might have been biased by edge-effects (taking account of pairs of points located mostly on the edges of the study area) and by the fact that high distance classes were mostly orientated toward the NW–SE direction. However, these points were kept in the semivariogram because we found no evidence of spatial anisotropy (dependence of the semivariogram on compass direction) in the lower distance classes semivariograms, and because these complementary values suggest that the semivariogram might have flatten off at large lag distances. The low number of sampling points ($n = 38$) may potentially have been a problem to obtain a reliable semivariogram estimates. However, the results of exploratory variography carried out by changing lag-distance intervals showed that our estimated semi-variogram was fairly stable and could be used for further modelling.

Because our measurements of attack intensity were not carried out at the same locations as the ONF measurements (Fig. 1), it was necessary to interpolate one set of values at the locations of the other set for further statistical crossings. In geostatistics, the procedure known as ordinary kriging uses the semivariogram estimated range, sill and directional anisotropy to build a model for spatial interpolation. We chose to interpolate our measures of percentages of attacked trees at the ONF sample points locations rather than the other way round for two reasons. First, because of the high risk of errors connected to the multiplicity of ONF

variables that should have been interpolated. Second, because the semivariograms of most ONF variables exhibited weak spatial dependence, which affects the quality of potential spatial interpolations. For kriging, we chose to ignore the non-stationary behaviour of the semivariogram of attack intensity because it was relatively small (the difference between the sill and the nugget was lower than 1 in the N–E correlogram). The model used for kriging was identified iteratively using VARIOWIN (Pannatier, 1996), selecting the best fit on the experimental semivariogram. Ordinary kriging based on that model was performed using the geostatistical package GSTAT (Pebesma & Wesseling, 1998). Kriging allowed us to interpolate attack intensity at the 63 points sampled by the foresters to assess site and stand characteristics. Kriging variance is known to increase dramatically outside boundaries defined by the sampling points (Isaaks & Srivastava, 1989). Therefore, only site and stand data located within the boundaries defined by the most external attack density sampling points were used for further analysis and modelling (54 points). Theoretically, the non-linear back-transformation via $\sin(x)$ of kriged estimates is biased (Isaaks & Srivastava, 1989) and should not be used. However, in our data set, measures of percentage of attack density were linearly related to their $\arcsin(x)$ transformed values ($r^2 = 0.997$; $n = 38$; $P < 0.001$) and had no extreme values (from 30% to 80%). The transformed percentage of attacked trees was therefore treated and interpreted as a direct measure of the percentage of attacked trees and back-transformed for display purpose in Fig. 3.

A preliminary stepwise multiple regression was carried out using the set of 54 interpolated values of attack intensity as the dependent variable and a set of explanatory variables consisting of altitude, slope, orientation, tree density, tree average height, yield class and average age (Table 1). This preliminary analysis showed that transformed percentages of attacked trees were related to tree density, and inversely related to yield class. However, the relation was not very strong ($r^2 = 0.17$; $n = 54$), especially for the yield class parameters. Because yield class is an index which reflects the relation between climate and soil characteristics and stand growth, we attempted to detail further the analysis of soil and temperature conditions along the transect to search for a hypothesis which could improve our model. Air temperature measurements along the transect showed a significant

Table 1 Parameters used as explanatory variables in the stepwise multiple regression analysis

Variable	Description
ALT	Altitude (m)
SLP	Slope (degrees)
OR	Orientation
DENS	Tree density (trees/ha)
AVHEIGHT	Average tree height (m)
YC	Yield class
AVAGE	Average age (years)
AVSLPX	Average slope within a circle of xmetres (degrees)
RGX	Number of <i>R. grandis</i> released within a circle of xmetres
RGOLDX	Number of <i>R. grandis</i> released within a circle of xmetres > 6 years before survey

(one-way ANOVA comparing average temperature measured by each recorder over the recording period: $F_{4,7080} = 2.766$; $P = 0.025$) but limited difference in temperature along the transect (1 °C of average difference between the highest and lowest point of the transect). Soil analysis results showed little change in soil texture (sandy loam textural class all over the transect) and organic matter, but considerable variations in average water loss (ranging from 30% to 70%). Organic matter was found to be very abundant everywhere (7% to 15%). Because soil texture and total organic matter content were fairly constant over the transect, topography was considered a more likely cause of variations in water content. There are two reasons why trees located on areas of high slope may tend to experience more severe summer drought. First, important rates of organic matter such as those observed in our samples dramatically decrease water availability to trees. Second, the observed soil texture drains fairly well, allowing water to flow easily towards the bottom of valleys, especially in areas of high slope. Consequently, we decided to estimate the average slope (based on a digital elevation model of the study area) within circles of increasing radius (from 0–1000 m in 50-m steps) centred on the ONF sampling points and to enter these variables in the stepwise multiple regression analysis (Table 1).

We used a circular moving window to estimate the number of *R. grandis* released within increasing distance (50 m, 100 m, 200 m, 300 m, 400 m, 500 m) around each ONF sampling points. This procedure was performed using all records or old records only (releases carried out >6 years before survey). These variables were also entered into the stepwise multiple regression analysis (Table 1).

Spatial autocorrelation in the dependent variable is a violation of the assumption of independence of observations and could have invalidated the level of significance of the linear models. A general framework for multiple linear regression is:

$$y_i = \mu + f(x_i) + e_i$$

with $i = 1, \dots, n$ where f is some function relating y to one or more x variables, μ is the overall mean of y and e_i is the error corresponding to the i -th observation. Among the usual assumptions of the linear model, variance among observations is constant [$Var(e_i) = \sigma^2$], and covariance among observations is zero [$Cov(e_i, e_j) = 0$], which is clearly violated in the presence of spatial autocorrelation. A spatial regression model can account for spatial autocorrelation by incorporating a model of covariance among observations into the general linear model framework (SAS MIXED procedure; Little *et al.*, 1996). In this case, the covariance among observations due to spatial autocorrelation is modelled by the function:

$$Cov(e_i, e_j) = \sigma^2 f(d_{ij})$$

and $j = 1, \dots, n$ where d_{ij} is the distance between the spatial location of the i -th and j -th observation and f is the spatial covariance function. The spatial regression model uses the sill, range and nugget of regression residuals to specify the

parameters of its spatial covariance model. These models are assumed to be isotropic (i.e. equivalent in all directions) and stationary, which was the case with the *D. micans* data. A spatial model of covariance was identified iteratively using VARIOWIN (Pannatier, 1996), selecting the model providing the best fit on the experimental standardized semi-variogram of multiple regression residuals. This spatial models of covariance, and linear model factors found using the stepwise multiple regression analyses, were introduced into the spatial regression modelling procedure to estimate actual levels of significance and unbiased coefficient estimates.

Finally, a layer of predicted values was built using the multiple regression model. Predicted values were estimated at the location of our measurements of attack intensity, for geostatistical analysis of residuals.

Results

Omnidirectional semivariogram estimators (Fig. 2) showed a strong spatial structure in attack intensity. Both estimators of the semivariance showed evidences of non-stationarity

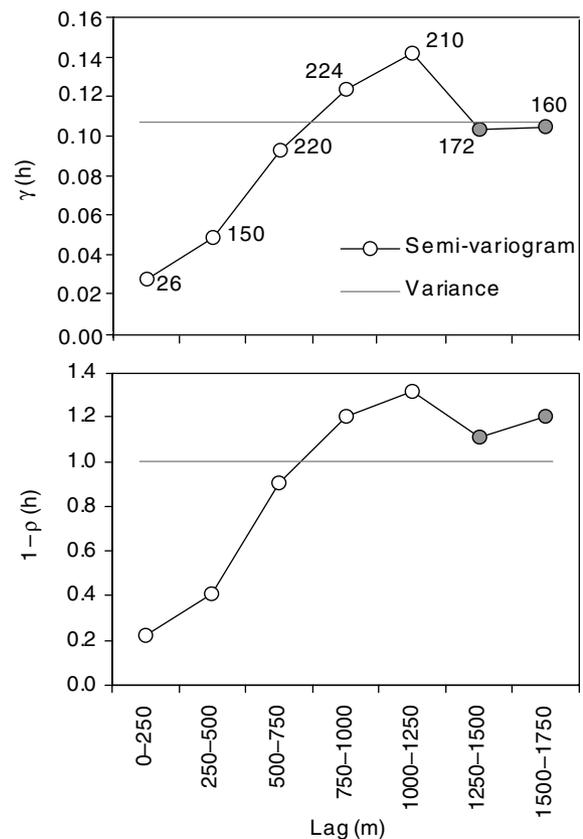


Figure 2 Semi-variogram and non-ergodic correlogram of the transformed percentages of attacked trees. The number beside each point represents the number of pairs of points used to calculate the estimators. The greyed points indicate estimates that may be biased by edge-effect. The semivariogram shows a strong spatial structure for distance lags below 700 m as well as evidence of non-stationarity (exceeding the overall variance, dotted line).

(the sill of the semivariogram was higher than the variance). A Gaussian model (Isaaks & Srivastava, 1989) with a sill of 0.094, a range of 780 m and a nugget of 0.026 provided the best fit to the experimental semivariogram and was used for ordinary kriging. However, the range estimate should be interpreted cautiously because it is based on points where the estimation may be biased as large distance classes were estimated on the basis of points orientated toward the NW–SE direction

The kriged population density surface was lowest on the south-east part of the study area. A local area of high population density was also located on the side of a steep slope as can be seen on Fig. 3, which clearly shows the gradient of population density explaining non-stationarity observed in the experimental semivariogram (Fig. 2).

Three main parameters were found to be significant in the stepwise multiple regression model (Table 2): tree density (DENS), the average slope within a 250-m radius (S250) and the number of *R. grandis* released within a 300-m radius >6 years before survey (RGOLD300). This relationship was stable in sign and significance for each parameter analysed separately versus the attack density. The semivariogram of standardized residuals was used to model the spatial covariance among residuals of the spatial regression model and showed lower levels of non-stationarity (Fig. 4). Tree density was not retained as a significant parameter by the spatial regression model (Table 3), illustrating the bias introduced by spatial autocorrelation in standard multiple regression residuals.

The distribution of attack intensities predicted by the spatial regression model including *R. grandis* (Fig. 5) was fairly close to the observed distribution except in the N–W, next to the plot boundary.

Discussion

Our analyses yield three major results: (i) stand colonization by *D. micans* has strong spatial structure; (ii) distribution was strongly correlated with site factors; (iii) 6–10 years after predator releases, *D. micans*' distribution was locally significantly correlated with *R. grandis*.

D. micans population attack density was thus strongly spatially structured at this scale in contrast with the results of a study carried out at a much smaller scale in which no spatial dependence was found in *D. micans* population density at the tree level (Gilbert *et al.*, 2001). Spatial structure in insect density has been observed at various scales for other pest species (Taylor, 1984; Liebhold *et al.*, 1994) and may be caused by a variety of factors. Theoretical models (Durrett & Levin, 1994; Holmes *et al.*, 1994) show that processes such as dispersal and impact of natural enemies may lead to patchy distribution within a completely homogeneous habitat (i.e. where establishment is uniform). Conversely, patchy population distribution may also be the consequence of a heterogeneous habitat. Spatial patterns revealed by geostatistics may thus be related to (i) insect behaviour, habitat characteristics and climate (affecting dispersal); (ii) habitat characteristics (affecting establishment); and (iii) competition or non-uniform impact of natural enemies (affecting dispersal and establishment via a possible impact on the size of the dispersing population). Although some of these factors were taken into account by the spatial regression model, the spatial structure revealed by our semivariogram is thus difficult to interpret because both dispersal and environmental correlation may be involved (Kendall *et al.*, 2000).

The second important outcome of our study is the quantitative impact of the average slope on pest abundance. The

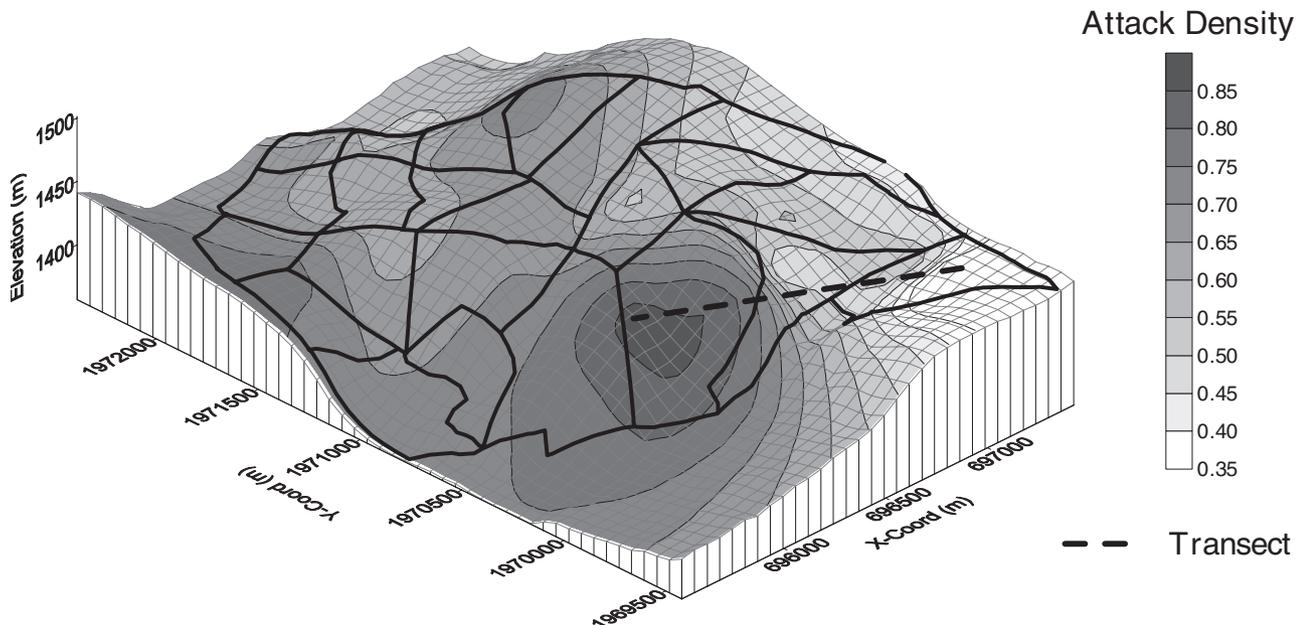


Figure 3 Result of the two-dimensional omni-directional kriging showing attack intensity (proportion of attacked trees) draped over the study area topography. The back-transformation of kriged values was performed for display purposes only.

Table 2 Multiple regression model showing the relationship between interpolated (transformed) percentages of attacked trees (TPATTA), trees density (LOGDENS is the log-transformed value of Tree Density), average *Rhizophagus grandis* released >6 years before survey within 300 m (RGOLD300) and average slope (AVSLP250) within 250 m

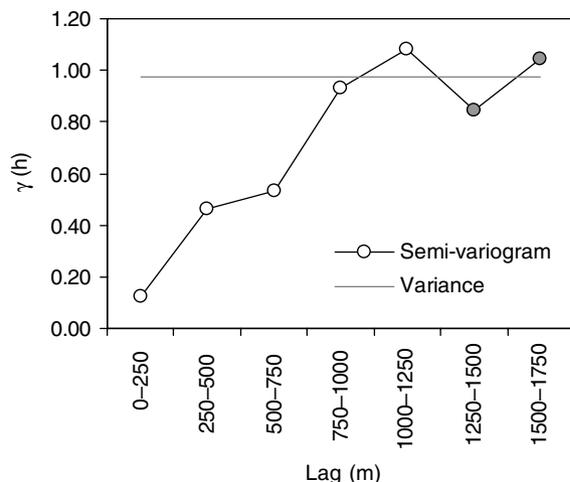
n	Constant (SE) <i>t, P</i>	LOGDENS (SE) <i>t, P</i>	RGOLD300 (SE) <i>t, P</i>	AVSLP250 (SE) <i>t, P</i>	SE of estimate	<i>r</i> ²	<i>F</i>	<i>P</i>
54	-0.110 (0.074) -1.474, 0.146	0.085 (0.025) 3.307, 0.0017	-3.41×10^{-4} (6.99×10^{-5}) -4.885, <0.001	0.027 (0.003) 8.045, <0.001	0.0348	0.670	34.488	<0.001

average-slope effect might be explained by trees located on steep slopes facing severe water stress in summer. There is a general agreement that droughts tend to facilitate outbreaks of many bark beetles (Mattson & Haack, 1987; Abbott, 1993; Lorio, 1996). Most historical records of *D. micans* outbreaks in Eurasia are related to severe drought (Grégoire, 1988). In our study, all the plots in the study area were subjected to fairly similar climatic conditions which could translate into variable water stress according to the slope. In this hypothesis, how water stress would influence tree susceptibility to *D. micans* is unclear. *D. micans* is highly resistant to chemical components found in the resin (Everaerts *et al.*, 1988). Resistance to attacks by *D. micans* may depend on the ability of trees to overwhelm colonizers with massive resin flow, and this trait might have high metabolic costs less likely to be met in the case of stress. In a recent review (Koricheva *et al.*, 1998), borers appeared as the insect guild that benefited most from host-plant stress. If this hypothesis is true, a distinctive characteristic of our study compared to historical records is that the potential effect of water deficit on tree resistance to *D. micans* could be effective at a very local scale (within 250 m).

To our knowledge, two other studies have reached similar conclusions in terms of slope and soil moisture content. Henriksen (1958) investigated 45 Sitka spruce plots in Denmark and observed that *D. micans* developed more slowly on flat temporarily waterlogged parts than on sloping

ground. Shavliashvili & Berozashvili (1976) studied the resistance of oriental spruce to bark beetles in relation to soil moisture and stand conditions and found that (i) the severity of pest damage (especially *D. micans*) was inversely related to soil moisture content and (ii) resistance decreased with increasing slope, especially on south-facing skeletal sandy loam soils. However, these two studies, as in the present one, were based on stands suffering severe water deficit (similar textural class) and high attack rates. It is unlikely that a similar relationship between attacks and slope could be found in places where water deficit is rare, and where other stress factors possibly play a more important role. It should be noted that local slope was in the set of variables of our first regression and had no statistical weight. It only became significant when it was averaged over a wider area (250 m radius), therefore reflecting a more general trend in the topography of the surrounding area.

The third significant outcome of this study was the link between attack intensity and early *R. grandis* releases measured 6–10 years later, within an optimal 300 m radius of influence. This is the first time that a direct, quantitative relationship has been shown to connect such a release and the subsequent attack intensity. However, the limited area of impact disclosed in our model was unexpected, especially because high levels of predator establishment were measured in other locations in the stand at the time of this study (unpublished). In 1997, 54% of the brood chambers that were analysed on 50 trees felled along the transect were colonized by *R. grandis*, and this proportion reached 63% the following year, when 65 brood chambers were opened at random in the stand. However, the *R. grandis* population may have stemmed from other releases carried out in other locations between 1991 and 1996. We have three main arguments in favour of such a local effect of *R. grandis*. First, *R. grandis* has been observed to disperse over 200 m annually following release (Grégoire *et al.*, 1985; Fielding

**Figure 4** Semi-variogram of linear model residuals used in the MIXED procedure showing a lower level of non-stationarity.**Table 3** Linear model parameters estimated using the MIXED procedure showing the relationship between interpolated (transformed) percentages of attacked trees, average *Rhizophagus grandis* released >6 years before survey within 300 m (RGOLD300) and average slope (AVSLP250) within 250 m

n	Constant (SE) <i>t, P</i>	RGOLD300 (SE) <i>t, P</i>	AVSLP250 (SE) <i>t, P</i>
54	0.1759 (0.030) -2.10, 0.04	-2.41×10^{-4} (1.15×10^{-4}) 3.43, 0.0012	0.017 (0.005)

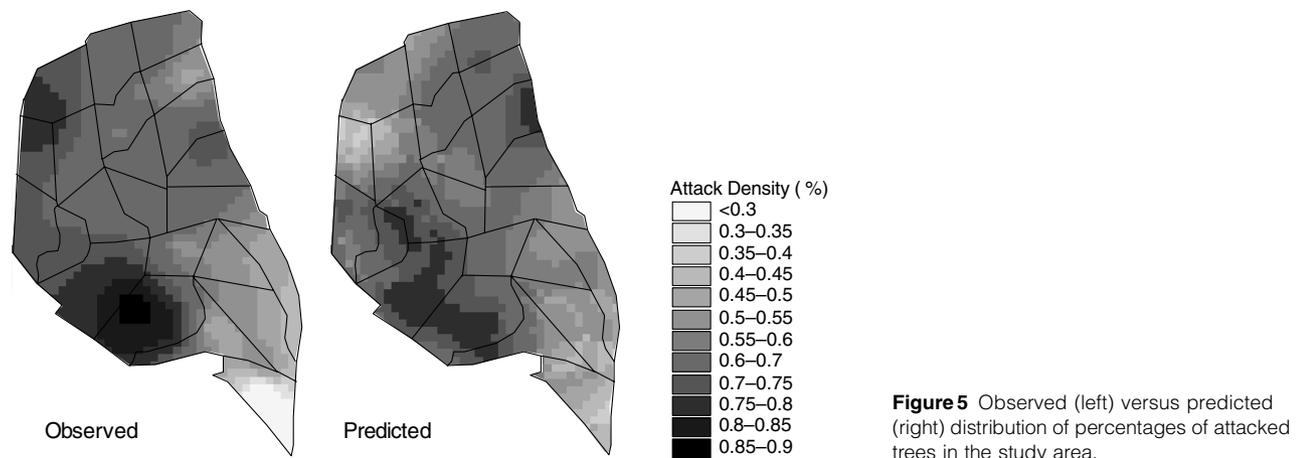


Figure 5 Observed (left) versus predicted (right) distribution of percentages of attacked trees in the study area.

et al., 1991b; Van averbeke & Grégoire, 1995) but, unless some preliminary flight is required (which has not been reported in the literature), the local abundance of suitable prey broods is likely to arrest dispersing insects before they have gone very far. Second, the insects only fly when wind speed is extremely low (Wyatt *et al.*, 1993), which favours random dispersal as opposed to directional flight following, or against, the wind. Therefore, insects from the next *R. grandis* generation following release have some probability to fly back to the release point (where they would be concentrated over a small area) instead of flying further away (in which case they would be diluted in a larger and still poorly colonized new area). Third, the time-lag between predator release and impact on prey abundances appears to be quite high, at least 6–8 years (unpublished observations since the first releases in France in 1983). Assuming a 200-m yearly progression, trees located within a 300-m range around early release points may thus have been colonized by *R. grandis* 2 years earlier than those further apart, which would explain the lower local percentages of attacked trees. A closer, spatially explicit analysis of predator dispersal and establishment following release might shed some light on this intriguing point, and perhaps also contribute to the establishment of more rational release procedures.

Our results may be very specific to this study area because the slopes sampled were mostly facing south-west, or because of the scale of the study. Nonetheless, limited spatial scale surveys are often the only form of investigation possible in the early stages of ecological studies, and they provide vital evidence for the creation of hypotheses about causality, which may be subsequently investigated. Further studies moving to a wider scale would allow comparison of the effect of different stand and site factors at various locations. It is also likely that other causal influences could be identified at a wider scale, either in areas where *D. micans* is endemic (e.g. site and stand conditions at the stand scale, or habitat fragmentation and connectivity) (Liebhold *et al.*, 1994; Sharov *et al.*, 1997; Coulson *et al.*, 1996), or in areas under biological invasion (e.g. effect of the road network permitting passive transportation of the insect through tim-

ber movement) as in the Republic of Georgia (Shavliashvili & Zarkhov, 1985) and in the UK (Bevan & King 1983).

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