

# Spatial pattern of invading *Dendroctonus micans* (Coleoptera: Scolytidae) populations in the United Kingdom

M. Gilbert, N. Fielding, H.F. Evans, and J.-C. Grégoire

**Abstract:** The spatial pattern of *Dendroctonus micans* (Kug.) attacks on individual spruce stands was analysed at the regional scale in Britain using data collected between 1982 and 1984 by the British Forestry Commission. These survey data reflect at least 10 years of *D. micans* spread, in the absence of natural enemies and of pest management control measures. A large-scale spatial gradient in the attack density at the stand level was identified and modelled. The large-scale spatial trend model explained 31.3% of the variability, and divided the study area in three separate areas: a zone where the insect was well established and where attack density presented low variations, a transition zone where attack density sharply decreased, and a zone not yet colonized. Attack density was related to site and stand factors, and to landscape neighbourhood in a linear spatial regression model. The factors correlated to attack density and the spatial autocorrelation structure of remaining variability were found to vary according to the zones, reflecting the predominance of different ecological processes occurring in colonized and uncolonized areas. The shape and orientation of the large-scale spatial model was shown to be mostly influenced by the spatial distribution of early attacks.

**Résumé :** La distribution spatiale des degrés d'infestations par l'hylésine géant de l'épicéa, *Dendroctonus micans* (Kug.), est étudiée à l'échelle régionale sur une base de données récoltées entre 1982 et 1984 par la Forestry Commission en Grande-Bretagne. Ces données reflètent 10 années de développement de l'insecte en l'absence d'ennemis naturels et de techniques de contrôle. Un gradient à grande échelle des degrés d'infestation est observé et modélisé. Ce modèle spatial permet d'expliquer 31,3 % de la variabilité et divise l'aire d'étude en trois zones distinctes : une zone où la population est bien implantée à un niveau stable, une zone de transition et une dernière zone dans laquelle l'insecte est pratiquement absent. Les résidus de ce modèle spatial sont reliés par un modèle de régression linéaire à des caractéristiques sylvicoles et stationnelles ainsi qu'à des éléments qui quantifient la structure du paysage. Ces facteurs ainsi que la structuration spatiale des résidus du modèle linéaire présentent des variations selon la zone qui sont mises en relation avec les processus écologiques dominants au sein des zones endémique ou en phase de colonisation. La forme et l'orientation du modèle spatial à grande échelle est principalement influencée par la distribution des attaques les plus anciennes.

## Introduction

Biological invasions are ecological phenomena characterized by the fast spread of organisms over large distances, in many cases helped by the absence of natural enemies in the newly colonized area (Hengeveld 1989). These invasions are particularly worrying when the colonizing organism is considered to be a serious agricultural or forest pest. The great

European spruce bark beetle *Dendroctonus micans* (Kug.) (Coleoptera: Scolytidae), which attacks apparently healthy spruce trees (*Picea* spp.) in Eurasia, was first observed in the United Kingdom near Ludlow (Shropshire) in 1982 (Fielding et al. 1991). Within a few weeks of subsequent surveys, it was clear that the insect had spread and had become established during previous years over a large part of the Welsh Marches and eastern and central Wales.

Anthropic factors (e.g., transportation of spruce timber) are known to be responsible for long-distance dispersal of *D. micans* in Eurasia when the beetle crossed large natural geographical barriers (invasion of the Caucasus area in the 1960s, of the United Kingdom in the 1970s). The same factors have probably played crucial roles in many other cases of long-distance movements. In the case of *D. micans*, dispersal and subsequent successful establishment was largely favoured by the fact that the beetle has a solitary colonization strategy. Females of *D. micans* emerge already fertilized from their brood gallery (Vouland et al. 1984), disperse by walking or flight, find a suitable host tree with a bias toward already attacked trees (Gilbert et al. 2001), establish a new gallery, and do not need to be joined by males to breed a new colony (Grégoire 1988). In the presence of host trees

Received 25 March 2002. Accepted 29 November 2002.  
Published on the NRC Research Press Web site at  
<http://cjfr.nrc.ca> on 26 March 2003.

**M. Gilbert<sup>1</sup> and J.-C. Grégoire.** Laboratoire de Biologie animale et cellulaire, C.P. 160/12, Université Libre de Bruxelles, 50, avenue F.D. Roosevelt, B-1050 Brussels, Belgium,<sup>2</sup> and Fonds National de la Recherche Scientifique, Brussels, Belgium.

**N. Fielding.** Forest Research, Shobdon, Leominster Hereford HR6 9PB, U.K.

**H.F. Evans.** Forest Research, Alice Holt Lodge, Wrecclesham, Farnham Surrey GU10 4LH, U.K.

<sup>1</sup>Corresponding author (e-mail: [mgilbert@ulb.ac.be](mailto:mgilbert@ulb.ac.be)).

<sup>2</sup>Address for correspondence.

and favourable climatic conditions, a single *D. micans* female, taking advantage of human transportation, is thus able to establish a new colony on its own.

Short-distance stand-to-stand dispersal in *D. micans* is probably accomplished mainly by flight of individual adults. Flight ability is assumed to be quite high (over 10 km in good climatic conditions; Forsse 1989), but this flight distance may be significantly lower where host trees are abundant (Gilbert and Grégoire 2003). Thus *D. micans* can be assumed to present "stratified dispersal" (Hengeveld 1989; Shigesada and Kawasaki 1997), which combines long-distance "jump spread" performed by passive transportation, with local population movements ("smooth spread") carried out by flight.

Populations of *D. micans* in Eurasia are usually kept at low levels by the specific predatory rhizophagid beetle *Rhizophagus grandis* Gyll., which has slowly followed *D. micans*' geographical expansion (Grégoire 1988). Outbreaks of *D. micans* may, however, occur in areas where the predator has not yet established, either because of its slower dispersal, as in the Massif Central (France; Granet and Perrot 1977), or because of a natural barrier that has not yet been crossed by the predator, as is the case in the United Kingdom.

The fact that *D. micans* seemed to have already invaded wide areas, in addition to the assumed absence of its known specific predator, was particularly worrying to the United Kingdom Forestry Commission. Extensive surveys were therefore undertaken between 1982 and 1984 with two main objectives (Fielding et al. 1991). Firstly, to delimit the extent of the infestation as a basis for establishing restrictions on movements of spruce, to minimize the risk of spread to other parts of the country through movement of timber. Secondly, to seek and destroy all attacked trees found during the surveys, in an attempt to reduce the overall population density of the insect. Over the 3 years, 13 500 sites were surveyed, and records of location, number of trees attacked by *D. micans*, and a series of other variables were collected. Dendrochronological measurements performed on a selected number of attacked trees were used to estimate that the first attack in the United Kingdom took place in 1973 or possibly earlier (King and Fielding 1989). This information indicated that the spatial pattern revealed by these survey data reflected at least 10 years of *D. micans* spread in the absence of natural enemies and of pest management control measures. The goal of the present study was to analyse the spatial patterns exhibited by the distribution of *D. micans* in relation to environmental and landscape features, thus providing a measure of early colonization by an exotic pest in a new environment where no factors restricting population development or dispersal are in place.

The spatial pattern of *D. micans* distribution and dispersal has already been studied at the plot scale (i.e., within 100- to 200-m spruce plots; Gilbert et al. 2001) and at the forest scale (i.e., within a 2 × 3 km study area; Gilbert and Grégoire 2003). Some attempt has also been made to build a regional-scale geographical information system (GIS) database for pest management purposes (Dolmans and Grégoire 1992). However, to date no study has analysed *D. micans*' spatial patterns at the regional scale, which is particularly important in the context of biological invasion involving

large-scale population movement by passive transportation, and individual movements carried out by flight. Furthermore, a regional study is close to the scale at which national pest management strategies tend to be implemented (O'Neill and Evans 1999), and analysis of regional patterns is therefore of great potential for risk assessment in recently colonized or vulnerable spruce forests, especially if patterns can be related to environmental characteristics. Analyses of spatial patterns in relation to environmental and landscape characteristics have been carried out in North America on other pest species such as the gypsy moth *Lymantria dispar* (Sharov et al. 1997; Liebhold et al. 1994) and the southern pine beetle *Dendroctonus frontalis* (Gumpertz et al. 2000). To our knowledge no comparable studies have been performed at a similar scale on a pest species in Europe.

This study explores the causal relationships that may explain attack levels within individual spruce stands by taking into account their spatial location, their landscape neighbourhood, and stand characteristics. The spatial location is relevant because it is assumed that stands located near or within a large-scale outbreak area will be more likely to be attacked than others located far from the colonization area. It is therefore essential to describe and analyse the large-scale distribution of attacks in the known infested area to assess the influence it may have on attack levels at the individual stand scale. The specificity of *D. micans* to the spruce genus, and its assumed limited flight ability in the wider landscape, makes the spatial structure of spruce ground cover a key factor potentially affecting the natural spread of the insect. An isolated spruce stand located a long distance from infested spruce stands is unlikely to be reached by flying insects. The spruce cover connectivity in the neighbourhood of a spruce stand may thus affect its probability of being attacked by insects moving in from already colonized distant stands. Finally, site conditions such as climate, or stand conditions through the resistance of host trees to the insect establishment, may affect the success of early colonizers, and therefore have an impact on the probability of finding an established colony in a given stand.

The influence of large-scale colonization patterns on attacks at the individual stand level was studied by modelling the regional distribution using a statistical spatial model, by analysing the model residuals in relation to landscape metrics of the neighbourhood spruce cover structure, and in relation to site and stand conditions using a linear mixed model. The remaining variability was analysed using spatial statistics.

## Material and methods

### Data

Data on *D. micans* were collected during field surveys conducted between 1982 and 1984 by the Forestry Commission. All spruce located within the study area were inspected for the presence of *D. micans* without regard to the size and status of planting. Counts of attacked trees, as well as other site data from 13 576 observations, were entered into a database. These data and the details of their collection are presented in Fielding et al. (1991).

The following variables were extracted from the database for the purpose of the present study: Ordnance Survey grid reference (accurate to 100 m), date of survey, percentage of

spruce within a stand, year of planting, yield class (a measure of current growth and yield relative to tree age and potential for growth to crop harvesting age), number of trees found attacked, estimated year of first attack, altitude, orientation, and slope. Extracted data were input into a geographical information system (GIS) database (ArcView GIS 3.1, ESRI, Redlands, Calif.).

*Picea* is essentially the only host genus utilized successfully by *D. micans*. A GIS layer of *Picea* patches over the study area was thus required for two reasons: firstly to allow raw observations to be converted into attack densities (see below), and secondly to allow measurements of the host-tree distribution landscape characteristics. However, existing land cover databases at British national scale do not usually differentiate between *Picea* spp. and other conifers. Hence a GIS layer of spruce cover over the study area was developed using the woodland survey database provided by the Woodland Survey Branch of the Forestry Commission, based on aerial surveys and records of any patch of woodland bigger than 0.5 ha. Three classes of woodland potentially containing spruce were extracted from this database: coniferous, mixed forest, and felled. To help identify patches containing spruce, two additional GIS databases were used. The first was a point database of the location of all spruce stands owned and managed by Forest Enterprise, a part of the Forestry Commission. All patches from the woodland survey database intersected by points from the Forest Enterprise database were classified as spruce. The second was the *D. micans* survey database outlined above, assuming that all patches of the forest woodland survey database classified as coniferous and intersected by a point visited during the survey contained spruce. This method may have misclassified some spruce patches, but is considered to give a reasonable figure of the spruce distribution in the study area. Contiguous patches sharing a boundary were merged to remove administrative boundaries separating spruce polygons.

The *D. micans* database records numbers of attacked trees observed in single point locations. It is difficult, however, to compare quantitative observations, such as the number of attacked trees, if the size of the spruce stand is unknown. Raw counts of attacked trees are more easily interpreted if these can be related to the host abundance at the point of observation, i.e., if they can be converted into densities (number of attacked trees per spruce area). Point-based values were therefore converted into values per patch using the spruce cover layer described above, by assigning summary values of *D. micans* to the underlying spruce patches they intersected, as shown in Table 1. The total number of attacked trees found per patch was divided by the patch area, thus converting values to a density, or number of attacked trees/km<sup>2</sup>. Of the 13 576 observations from the *D. micans* survey database, 1433 did not intersect patches from the woodland survey database. These points representing 10.5% of survey observations were probably isolated trees or very small patches (<0.5 ha) and have not been taken into account in this study, mainly because they can not be converted into densities (number of attacked trees per spruce area) and compared with other observations made in spruce patches. In total, 12 143 out of 13 576 individual point observations were thus summarized into 1129 records associated with individual noncontiguous spruce patches (Fig. 3).

## Analysis

Insect count data are known to present strong proportionality between local mean and variance, a highly left-skewed frequency distribution, and tend to be far from normal (Taylor 1961). This was the case with the current set of attacked-tree densities; to reduce the proportionality between mean and variance and to normalize the frequency distributions of patch attack densities, attacked-tree densities were log-transformed ( $\log_{10}(x + 1)$ ).

The spatial dependence of the log-transformed densities of attacked trees was analysed using geostatistical tools allowing quantification of the statistical spatial dependence of sampling points replicated through space. A summary of the suitability of such methods in applied ecology is given in Rossi et al. (1992), with a more comprehensive approach presented in Isaaks and Srivastava (1989) and extensive theoretical details in Cressie (1993). Statistical spatial dependence is important to the analysis of spatial data sets firstly for the insight it provides on the variable under study when subject to interpretation (Rossi et al. 1992) and secondly because it represents a bias to the assumption of independence among samples that needs to be taken into account in parametric statistical analyses such as linear models (Lennon 2000; Keitt et al. 2002). In the present study, standardized semivariograms calculated using the VARIOWIN software (Pannatier 1996) were used to explore the statistical spatial dependence.

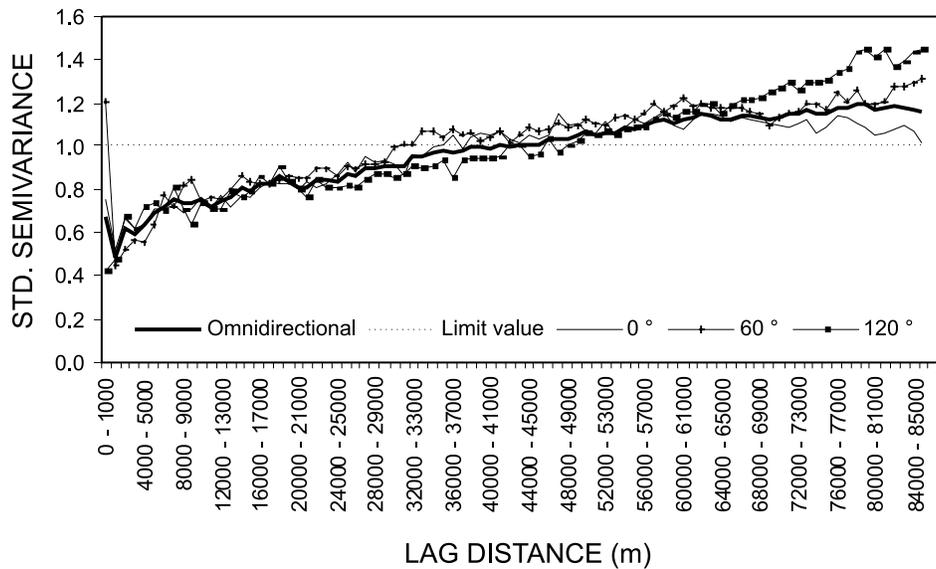
The standardized semivariogram of attack density (Fig. 1) showed evidence of nonstationarity (values >1 for large lags and no levelling-off plateau). Nonstationarity is typically caused by a spatial trend, or a gradient over long distances, that links local values to location. In the presence of a large-scale gradient, the differences among values separated by long distances can be due to differences between the respective local means, and not to differences associated with the variable's spatial continuity, thus introducing a bias in the estimation of the semivariance. The spatial trend is clearly visible in the distribution of infested ( $\log(\text{attacked-tree density} + 1) > 0$ ) and uninfested patches ( $\log(\text{attacked-tree density} + 1) = 0$ ) that show one main area where most patches are infested, one area where infestations are very rare and a transition area (Fig. 3). Such distribution suggested that the pattern of invasion could be explored by an approach derived from works carried out by Sharov et al. (1997) on the invasion of the Gypsy moth *Lymantria dispar* (L.) in Virginia and West Virginia, who showed that the effect of landscape characteristics on the pest pheromone captures differed according to three zones at the expanding front of the population: infested, transition, and uninfested zones. We assumed that a similar pattern of infested, transition, and uninfested zones was present in our data, to test if the relationship between attacked-tree density and site, stand, and landscape factors would vary according to these zones. The goal of the spatial trend model was thus firstly to model the large-scale variability in attacked-tree densities and secondly to delimit the infested, transition, and uninfested zones. Two different models were tested for this purpose.

The first model assumed that the two-dimensional space can be divided into three zones (Fig. 2, model a): a zone of constant level of attacked-tree densities (zone I), a transition zone where the attacked-tree density decreases (zone II), and

**Table 1.** List of variables used from the *D. micans* point database and their equivalent summarized per spruce patch.

Variables per point	Statistic used	Variables per spruce patch	Abbreviation
x coordinate	Average	Average x coordinate	XCoord
y coordinate	Average	Average y coordinate	YCoord
No. of attacked trees	Sum	Sum of attacked trees observed found in the patch	ATTA
Spruce percentage	Average	Average spruce percentage	SPC
Plantation year	Average	Average plantation year	PLYR
Yield class	Average	Average yield class	YC
Elevation	Average	Average elevation	ALT
Slope	Average	Average slope	SLP
—	—	Patch area	AREA
—	—	Attack density (attacked trees from ATTA/km <sup>2</sup> from AREA)	ADENS

**Fig. 1.** Standardized semivariogram of log-transformed attack densities over different directions (0°, 60°, and 120°) and over all directions (omnidirectional). This experimental standardized semivariogram shows a positive spatial autocorrelation for distance lags lower than 35 km, and evidence of nonstationarity, as shown by its shape, that does not level off at the limit value of one, and keeps increasing over long distances.



a zone not yet infested (zone III). The model was based on the following equations:

In zone I:

$$PD = a$$

In zone II:

$$PD = a \exp 10 \left( -\frac{d^2}{b} \right)$$

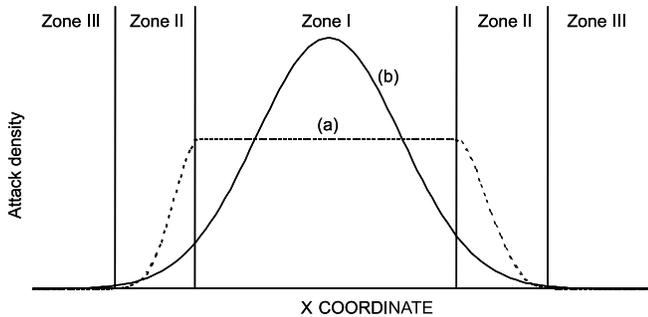
In zone III:

$$PD = 0$$

where PD is the predicted log-transformed attacked-tree density, *a* is the height of the plateau, *b* is a measure of the decreasing intensity (the greater the value of *b*, the longer the distance to decrease from *a* to 0), and *d* is the distance from the plateau. The limit between zones II and III was arbi-

trarily set as the distance corresponding to a very low predicted attacked-tree density ( $\log(\text{attack density} + 1) = 0.001$  corresponding to 0.0023 attacked trees/km<sup>2</sup>). To build this model, we had to define the two-dimensional boundary of zone I, within which attack density would be assumed to be constant. To determine this boundary, log-transformed attack densities were smoothed by 30 km radius circular averaging windows in a grid of 1-km<sup>2</sup> cells. Isolines of attacked-tree densities were then estimated on the basis of this grid (Fig. 3). An averaging radius of 30 km was chosen, because a smaller radius generated very irregular isolines (presence of islands, gaps, or folds) whereas a higher averaging radius generated isolines not affected by precise details of the observed distribution. The next step was to choose one of these isolines that would best delineate the infested area. All patches were firstly classified as infested (attacked-tree density > 0) or uninfested (attacked-tree density = 0). For each isoline, the number of patches that would be mis-

**Fig. 2.** One-dimensional view of the two models. Model (a) divides the space into three areas: zone I where the attack density is at a constant plateau, zone II where the attack density drops off with a normal curve, and zone III that is not yet colonized. Model (b) assumes a diffusive dispersal process from a central source with a two-dimensional normal function.



classified if the isoline was used to delineate the infested area was estimated (a patch is considered as misclassified if it is uninfested within the area delineated by the isoline, or is infested outside this area). The isoline corresponding to the lowest number of misclassified patches was then used to delineate the infested area. The isoline of  $0.0750 \log(\text{attacked-tree density} + 1)$  corresponding to an average density of  $0.188$  attacked trees/km<sup>2</sup> presented the minimum number of misclassified spruce patches inside and outside the area delineated by the isoline boundaries (Figs. 3 and 4). Using this boundary and the Gaussian decreasing function used in zone II, a two-dimensional model was fitted to the distribution of attack densities, and the parameters ( $a$  and  $b$ ) were iteratively adjusted to provide the best fit. This model captured fairly well the overall infestation distribution (Fig. 5, model  $a$ ) and allowed to delineate the three zones. However, this model did not account for spatial variations in attacked-tree densities that may have occurred within the plateau.

A second model was thus tested, which had the shape of a simple two-dimensional normal distribution surface (Fig. 2, model  $b$ ) with an elliptic section (i.e., not equal in all directions). The predicted value of the model was calculated for point  $(x, y)$  according to the following function:

$$PD = a \exp 10 \left( -\frac{d^2}{b} \right)$$

where

$$d^2 = x'^2 + (ry')^2,$$

$$\begin{cases} x' = (x - x_0) \cos \alpha + (y - y_0) \sin \alpha \\ y' = (y - y_0) \cos \alpha + (x - x_0) \sin \alpha \end{cases}$$

where PD,  $a$ , and  $b$  are described as above,  $x_0$  and  $y_0$  are the coordinates of the ellipse centre,  $\alpha$  is the angle between the ellipse main axis and north, and  $r$  is the anisotropy ratio (ratio between the ellipse main and secondary axes). This model was fitted to the distribution of attack densities, and the parameters were adjusted iteratively to provide the best fit. The decrease function used in both models corresponds with a Gaussian distribution and is based on the assumption that populations follow Skellam's model:

$$\frac{\partial n(x, y, t)}{\partial t} = D \left( \frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) + rn$$

where  $n$  is population density at spatial coordinates  $x, y$ , and time  $t$ ,  $D$  is the diffusion coefficient that measures dispersal rate, and  $r$  is the growth rate (Shigesada and Kawaski 1997). This differential equation translates at any given time into a Gaussian distribution when the population is assumed to start from a single point source. Although this model had a better overall fit than the first, it did not render the sharp decrease in infestations at the edge of the main colonization area and it tended to overestimate attacked-tree density of patches located outside the main colonized area where infested patches are more scarcely distributed (in zones II and III).

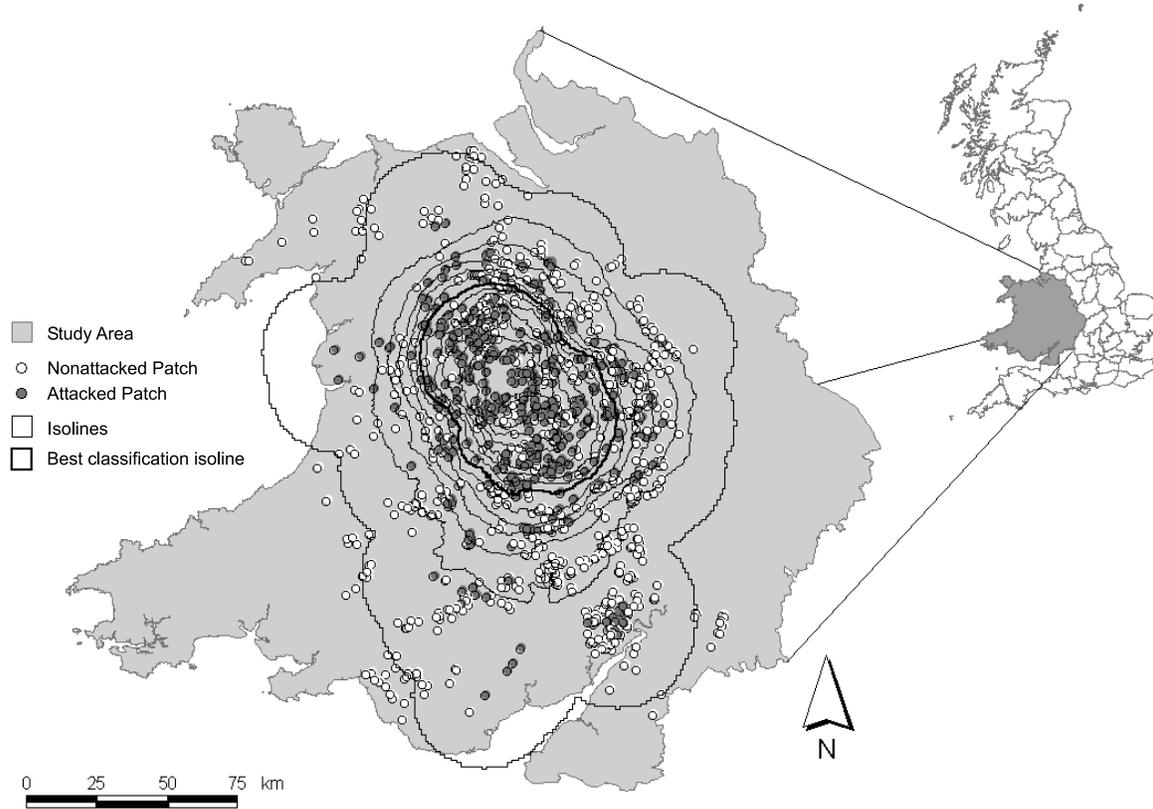
A linear combination of the two models was then tested selecting the parameters providing the best fit (Fig. 5, model  $c$ ). The combined model, which had a better fit than the individual ones, fulfilled the two goals of the spatial trend model: delimit the infested, transition, and uninfested zones and model large-scale variations in attacked-tree densities between and within the zones. Standardized semivariograms of the residuals of the combined spatial trend model showed no evidence of nonstationarity, indicating that long-distance gradient variability had been fully removed (Fig. 6). Further analyses thus focused on these spatial model residuals as a measure of the remaining variability in attack density.

Landscape metrics of the spruce cover in each patch neighbourhood were determined using the following method. The analysis commenced with the GIS layer of 1129 noncontiguous spruce patches where information on *D. micans* and site and stand conditions had been summarized. For each of the  $p_i$  patches, all spruce patches found within a given neighbourhood distance ( $d$ ) of its boundaries were extracted and landscape metrics were calculated on these  $n_{pi}$  extracted polygons and added to the  $p_i$  polygon table record. Neighbourhood distances of 1, 2.5, 5, 10, and 20 km were used. Several different landscape metrics can be calculated on the basis of a few patches, many of which are strongly correlated and redundant (Rijters et al. 1995), thus the choice of the metrics to use should reflect some explicit hypothesis about the pattern of interest (O'Neill et al. 1988). In this case it was decided to restrict measures to four different metrics that were believed to influence the dispersal of *D. micans*:

- (1) MPAR: the mean patch area, average area of the  $n_{pi}$  patches found in the neighbourhood,
- (2) PD: the patch density, the number of patches ( $n_{pi}$ ) per square kilometre in the neighbourhood,
- (3) ED: the edge density, the total perimeters of the  $n_{pi}$  patches divided by the neighbourhood surface,
- (4) MSI: the mean shape index, which measures the average  $n_{pi}$  patches shape complexity on the basis of perimeter/area ratio. It is lowest when all patches are circular and increases as they become increasingly noncircular (McGarigal and Marks 1995).

The assumption behind the choice of the MPAR is that small patches should favour long-distance dispersal because, once colonized, they are more quickly exploited than larger

**Fig. 3.** Study area and its location within the United Kingdom. The distribution of attacked (shaded circles) and nonattacked (open circles) spruce patches is overlaid by density isolines and the best classification isoline (in bold) used to delineate the first spatial trend model. The best classification isoline minimizes the total number of misclassified patches (patches are considered as misclassified if they are uninfested within the area delineated by the isoline, or are infested outside this area).

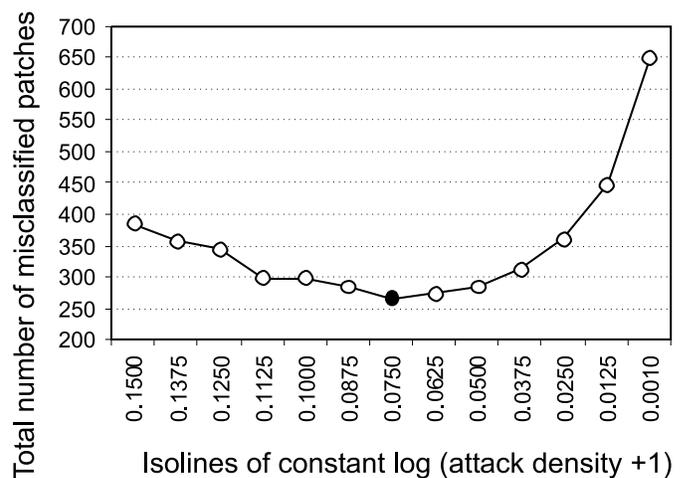


ones, thus forcing the insects to disperse more quickly to other stands. The assumption behind the choice of the other indices is that high edge density, patch density, and shape index should favour overall connectivity between spruce patches by flying insects. An additional measure of the shape index of the 1129 noncontiguous individual spruce patches was carried out and added to the table of records. All landscape metrics were calculated using the Patch Analyst (Elkie et al. 1999) which is an ArcView extension developed on the basis of the Fragstat spatial pattern analysis program (McGarigal and Marks 1995).

Site and stand factors (mean spruce percentage, mean plantation year, mean yield class, mean altitude, mean slope) were already in the Forestry Commission database and required no additional calculations.

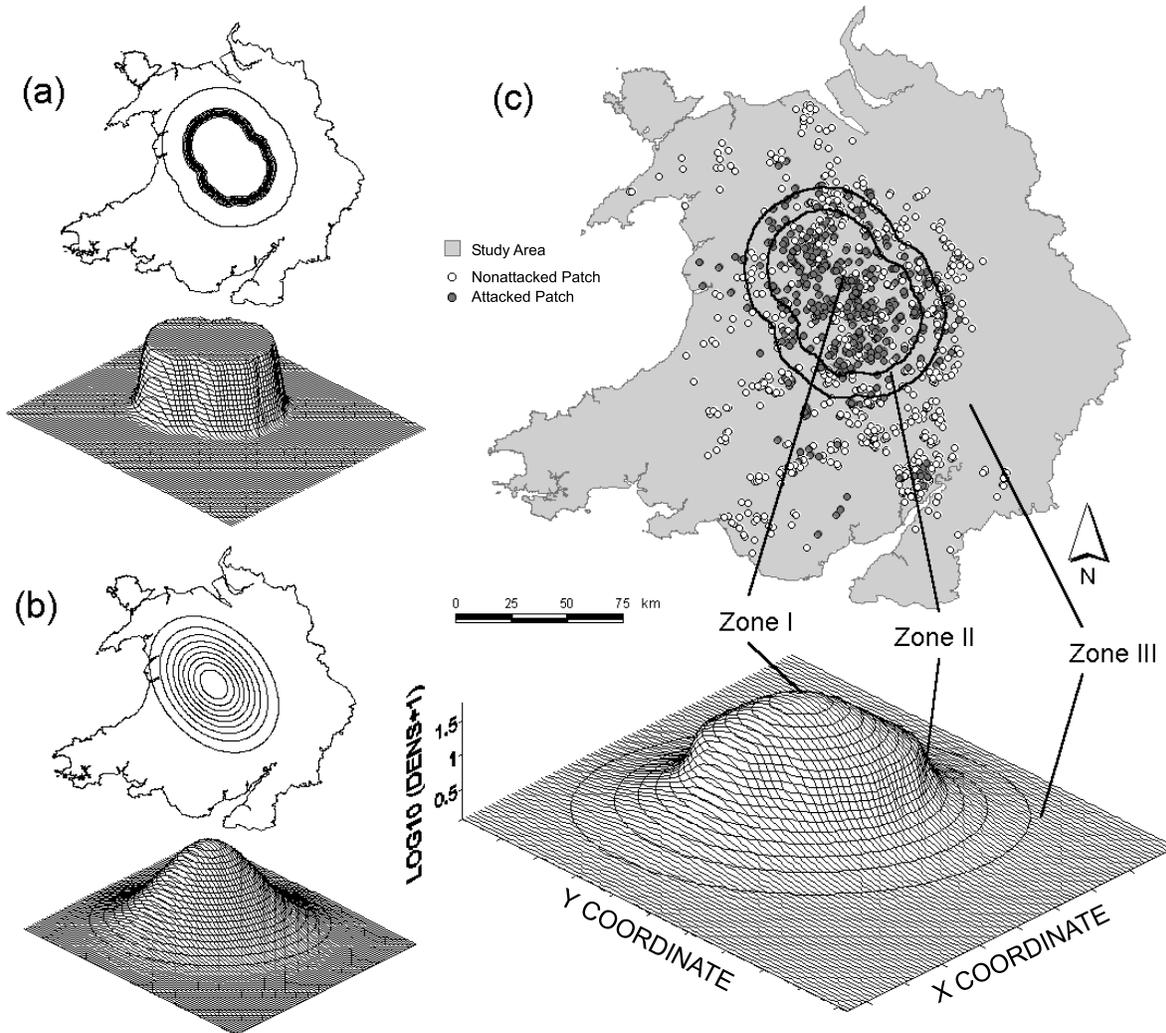
Stepwise multiple regression analyses were carried out using the residuals of the spatial trend model as dependent variables, and the set of landscape metrics and site and stand factors as explanatory variables. Four models were built: one for the whole survey area and one for each of zones I, II, and III, separately. This strategy was based on the assumption that causal relationships may appear to be different in an established infested area (zone I), a recently colonized area (zone II), and an almost uncolonized area (zone III). The dependent variable, and most likely explanatory variables, were strongly autocorrelated, which represents a bias to the assumption of independence among samples and will

**Fig. 4.** Evolution of the total number of misclassified patches for boundaries isolines. The isoline of 0.0750 log(attack density + 1) corresponding to 0.188 attacked trees/km<sup>2</sup> (solid circle) minimizes the total number of misclassified patches inside and outside the area delineated by its boundaries.



inflate the level of significance of the multiple regression model and of the individual factors. Clifford et al. (1989) proposed a method to account for spatial autocorrelation in bivariate correlations, but no general model has yet been

**Fig. 5.** Views of the three models. The first model (a) shows a flat plateau delimited by an isoline of the observed attack density (zone I), sharp decreasing normal curves from the plateau boundary that define zone II (buffer of 9.5 km from zone I), and zone III. The second model (b) shows an anisotropic (i.e., not equal in all compass directions) two-dimensional normal curve. The curve main axis is oriented toward the 135°N direction, and the secondary axis is oriented toward the 225°N direction. The combined model (c) (only isolines delineating the three zones are presented in the map) delimit the infested, transition, and uninfested zones and model large-scale variations in attacked-tree densities between and within the zones.

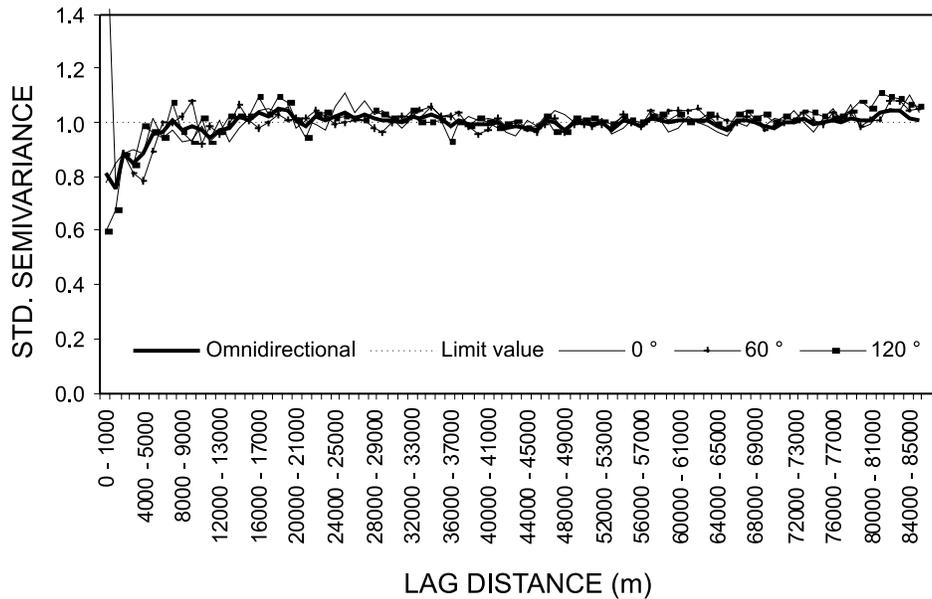


proposed to account for spatial autocorrelation in dependent and independent variables in linear models. In a recent paper, however, Keitt et al. (2002) compared several statistical spatial models designed to mitigate the impact of spatial autocorrelation in such environment–abundance statistical modelling. They conclude that there is a radical difference between independent models and spatial models, and that although different spatial models differ in their mechanistic interpretation, their conclusions are typically very similar. Therefore, we used the SAS MIXED procedure to account for spatial autocorrelation in the dependent variable by incorporating a model of covariance among observations into the general linear model framework (Little et al. 1996). In this case the covariance among observations due to spatial autocorrelation is modelled by the function:

$$\text{cov}(e_i, e_j) = \sigma^2 f(d_{ij}), \quad j = 1, \dots, n$$

where  $e_i$  is the error corresponding to the  $i$ th observation,  $d_{ij}$  is the distance between the spatial location of the  $i$ th and  $j$ th residual, and  $f$  is the spatial covariance function. The SAS MIXED procedure uses the estimated sill, range, and nugget from the multiple 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 spatial trend model residuals. One spatial covariance model per multiple regression was identified using a combination of fit-by-eye and least squares approaches and selecting the model providing the best fit on the experimental standardized semivariogram of the multiple regression residuals (scale, nugget, range, and  $R^2$  of the fit were obtained). Factors selected by the stepwise multiple regression analyses and best-fit spatial models of covariance were introduced into the SAS MIXED procedure to estimate levels of significance and coefficient estimates.

**Fig. 6.** Standardized semivariogram of the spatial trend model’s residuals, showing spatial autocorrelations that level off at a range distance of 9 km and no evidence of nonstationarity.



Finally, the potential reasons for the observed shape of the large-scale spatial trend in attack densities were explored. As mentioned above, the estimated year of first attack was recorded in the *D. micans* Forestry Commission database. This dating was made at the time of survey by examination of occluded attacks in relation to tree age. The goal of dating the attacks was to determine the first appearance of *D. micans* in a given locality, thus indicating the rate of spread away from the earliest occurrence. However, these data were not used in this study because it is not possible to date attacks precisely using visual observation of *D. micans* occluded attacks on standing trees, especially when trying to date back attacks older than 2 years. Despite these reservations, it was felt that the estimated year of first attack could provide qualitative information on the initial distribution of attacks. In particular, attention was focussed on whether the shape of the long-distance gradients could have been caused by the spatial distribution of initial attacks, or if it was the consequence of population movements in particular directions. To test this, all attacks dated before 1981 (before the first survey) were grouped in an “initial attacks” subset, which was mapped to support the discussion on early attacks distribution.

**Results**

The distribution of attacked patches (Fig. 3) showed a clear directional trend, and an almost elliptic shape oriented north–south. The proportion of attacked versus nonattacked patches was fairly constant within the central area, decreased sharply at a certain distance from the centre, and was dependent on direction (short distance over the 45°N direction, a longer distance over the 135°N direction). Some isolated populations were observed outside this central area, such as in the S–SW.

The best fit for the first spatial trend model returned the following parameters: *a* (height of the plateau) = 1.445; *b* (measure of dispersal) =  $1.3 \times 10^{-8}$ . Using these parameters,

**Table 2.** Coefficient of determination and overall significance of the multiple regression models carried out over the whole area and into the three separated zones.

Zone	<i>R</i> <sup>2</sup>	df	<i>F</i>	<i>P</i>
All	0.084	1051	19.182	<0.0001
I	0.130	351	13.110	<0.0001
II	0.135	178	9.239	<0.0001
III	0.060	534	11.388	<0.0001

zone II was delimited by a 9.5-km-wide strip around the plateau boundaries, which corresponded to a predicted  $\log(\text{attack density} + 1)$  of 0.001 (corresponding to 0.0023 attacked trees/km<sup>2</sup>). This spatial trend model, presented in Fig. 5, model *a*, has an *R*<sup>2</sup> value of 0.263. The best fit for the second spatial trend model returned the following parameters: X-COORD of the centre (*x*<sub>0</sub>) = 323 990; Y-COORD of the centre (*y*<sub>0</sub>) = 294 022; anisotropy ratio (*r*) = 1.497; orientation of the main axis (*α*) = 135°N; maximum  $\log_{10}(\text{dens})$  at the centre (*a*) = 1.969; measure of dispersal (*b*) =  $1.9 \times 10^{-10}$  (Fig. 5, model *b*). The *R*<sup>2</sup> of the second spatial trend model was 0.307. The linear combination of the two spatial models providing the best fit was found using the following parameters: PD = 0.265 MODEL1 + 0.690 MODEL2 + 0.045 and had an *R*<sup>2</sup> of 0.313. This model captured the sharp decrease in infestation levels at the edge of the main colonization area as well as the variations in attacked-tree densities within the zones (Fig. 5, model *c*). The standardized semivariogram (Fig. 6) of the residuals of this model showed clearly that any large-scale gradient has been fully removed by the spatial trend model (compare with Fig. 1).

The coefficient of determination and overall significance of the four multiple regression models (all zones, zone I, II, and III), relating spatial trend model residuals to site, stand, and landscape factors, are presented in Table 2. The individual factor parameters and levels of significance are found in

**Table 3.** Individual effects of the multiple regression models with spatial model of covariance, estimated on the overall area (all zones), and over the three separate zone subsets (zone I, II, and III).

	Effect	Estimate	SE	df	<i>t</i>	<i>P</i>	<i>P</i> SMR
All zones	PLYR	-0.014 660	0.002 028	1051	-7.230	<0.0001	<0.0001
	ALT	-0.001 108	0.000 305	1051	-3.630	0.0003	<0.0001
	PD1*	0.233 000	0.080 600	1051	2.890	0.0039	<0.0001
	MPAR1†	-0.000 744	0.000 264	1051	-2.810	0.0050	<0.0001
	MSI‡	0.067 630	0.034 030	1051	1.990	0.0471	0.0498
Zone I	PLYR	-0.023 770	0.004 497	351	-5.290	<0.0001	<0.0001
	ALT	-0.002 342	0.000 728	351	-3.220	0.0014	0.0009
	PD1*	0.507 200	0.190 500	351	2.660	0.0081	0.0017
	MPAR1†	-0.001 668	0.000 581	351	-2.870	0.0043	0.0027
Zone II	PLYR	-0.016 460	0.004 838	178	-3.400	0.0008	0.0008
	ALT	-0.001 604	0.000 623	178	-2.570	0.0109	0.0007
	MSI§	0.220 900	0.110 200	178	2.000	0.0466	0.0186
Zone III	PLYR	-0.007 226	0.001 988	534	-3.640	0.0003	<0.0001
	MSI‡	0.047 910	0.026 590	534	1.980	0.0482	0.0441
	PD10	1.446 800	0.695 000	534	2.080	0.0379	0.0001

**Note:** The equivalent standard multiple regression model factors levels of significance (*P* SMR) are given for comparison purpose.

\*Patch density within a 1-km neighbourhood.

†Mean patch area within a 1-km neighbourhood.

‡Patch mean shape index.

§Mean shape index of patches found within a 1-km neighbourhood.

||Patch density within a 9-km neighbourhood.

**Fig. 7.** Standardized semivariograms of multiple regression residuals in the three zones (□) and their respective spherical models (broken line). The figure shows that zones differ in their range varying from 4270 to 7228 m (distance where the curve reaches the value of 1) and in their spatial autocorrelation intensity (as measured by the y axis intercept).

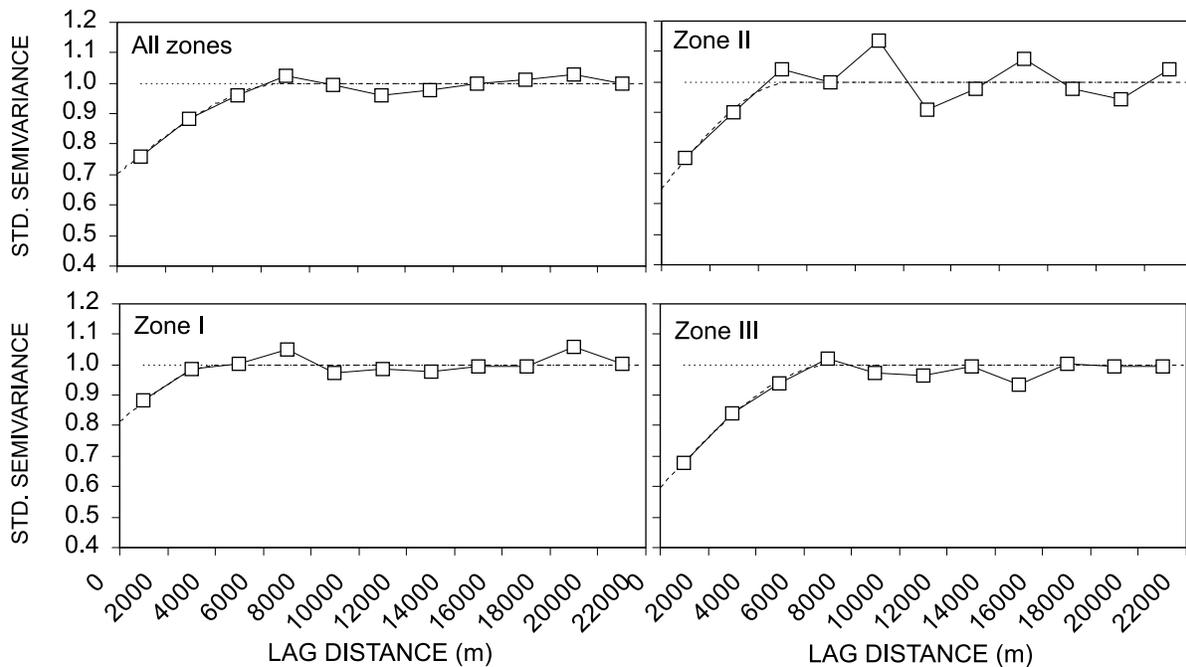
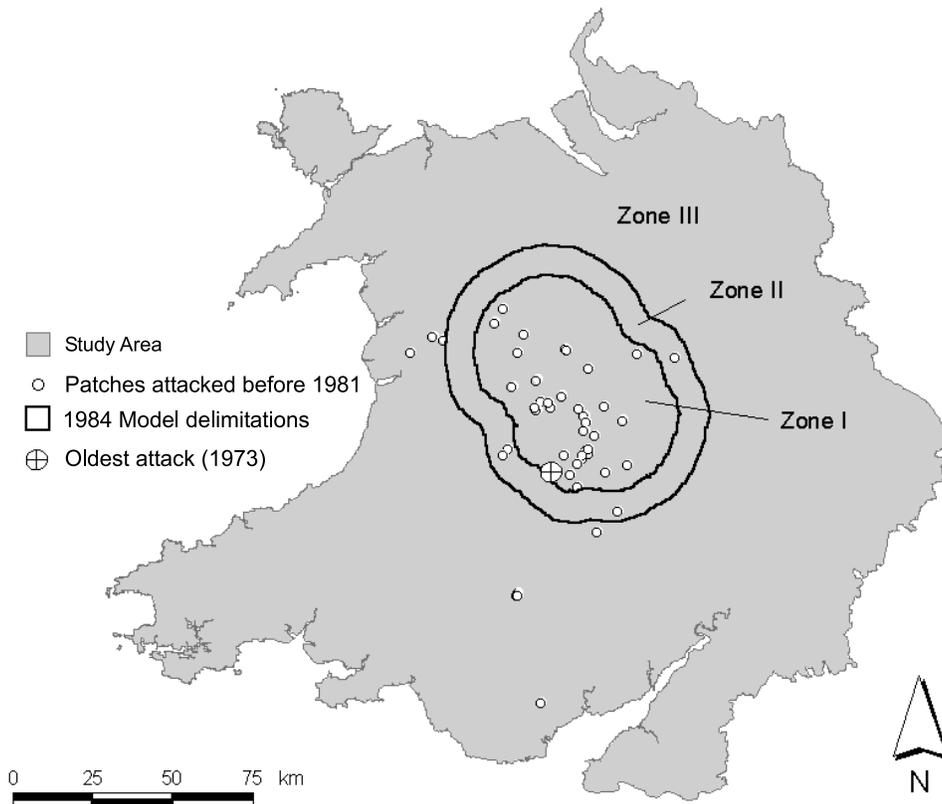


Table 3, and the spatial models of covariance used for each of the four models are presented in Fig. 7. The best fit between spatial covariance models and standardized semivariograms of multiple regression residuals was found using spherical models (Fig. 7). These spherical models differed in

their range and in their nugget value (all zones: range = 7050 m, nugget = 0.721,  $R^2 = 0.934$ ; zone I: range = 4270 m, nugget = 0.814,  $R^2 = 0.750$ ; zone II: range = 5390 m, nugget = 0.626,  $R^2 = 0.629$ ; zone III: range = 7228 m, nugget = 0.597,  $R^2 = 0.932$ ), which is an inverse

**Fig. 8.** Map of initial attacks distribution showing two isolines delineating zones I, II, and III of the spatial trend model.



measure of the spatial dependence. The spatial autocorrelation is measured by the difference between the sill (in this case always equal to 1) and the nugget, thus zone III presented the highest level of spatial autocorrelation over the longest range and zone I presented the lowest spatial autocorrelation over the shortest range.

Although the significant variables were not similar in the separate zones (Table 3), a common feature was that factors associated with high connectivity (such as a high patch density and low average patch area in zone I, high shape index in zone II, and high patch density and shape index in zone III) were positively related to the spatial trend model residuals. This was also observed in the overall model (all zones) in which the spatial trend model residuals were positively related to high patch density, to low patch area in the close neighbourhood, and to high shape index. The effect of planting year and altitude is present in the overall model, and in the individual zones, except in zone III where altitude is not significantly related to the spatial trend model residuals. The comparison between  $P$  values provided by the SAS MIXED procedure with those estimated by the standard multiple regression showed that taking the spatial structure of errors into account almost always reduced the significance of individual factors. The model that sums predictions made by the spatial trend model ( $R^2 = 0.313$ ) to predictions made by the linear model over all zones ( $R^2 = 0.084$ ) had a coefficient of determination of 0.384.

Finally, the spatial distribution of attacks dated before 1981 (Fig. 8) showed that the overall direction of the spatial trend model of 1984 attack density coincided with the over-

all direction of early attacks, although several isolated points could already be observed.

## Discussion

A significant proportion of the variability in spruce patch attack density can be explained by large-scale spatial patterns, neighbourhood spruce cover structure indices, and site and stand conditions (altitude and plantation year, respectively).

The largest proportion of the variability in attack density is explained by the spatial trend model, which captures fairly well the large-scale gradient, despite few isolated populations not being predicted by the model (e.g., groups of attacked patches located far from the best classification isoline in Fig. 2). This pattern of small isolated populations located far from the main one is typical of stratified dispersal and tends to support the hypothesis that *D. micans*' dispersal combines long-distance jump spread resulting from anthropic transportation with local dispersal by flight. The results presented here suggest that the general shape and orientation of this large-scale model could be explained partially by the pattern of initial attacks dated before 1981. The shapes of the two distributions do not, however, coincide, and attacks tend to have moved more toward the north than expected from the initial attacks. Mountains located in the west of the study area and oriented along a north-south direction could have constituted a natural barrier to the autonomous dispersal of *D. micans*, and contributed to a directional bias in the orientation of the attacks. However, this

does not explain why initial attacks are oriented in such a way, especially when looking at the location of the oldest attack dated 1973. Apart from the possible effects of natural barriers such as the mountains in the west, there appear to be no large-scale environmental factors that may explain such a directional trend in the distribution of *D. micans* attack densities. It is more likely that transportation of infested timber may have played a significant role in spreading the insect in such a way. There may be two nonexclusive hypotheses, not tested in the present study, that may have produced such a pattern. Firstly, the pattern may be the result of stochasticity of long-distance movements by passive transportation, the very first attacks being distributed by chance toward the observed north-south direction, and subsequently determining the spatial distribution pattern. The second hypothesis is that the observed pattern may have been influenced by the spatial pattern of human activities, such as the locations of sawmills, or the distribution of main roads used by trucks carrying infested timbers, implying possible repeated movements from the initial epicentre because of the implied higher frequency of movements of infested timber along particular routes.

The spatial trend model divides the study area in three separate geographical zones: a first area where most patches are infested, surrounded by a second area where infestation sharply decreases, and a third area where the insect is nearly absent. These zones serve as a framework to discuss results under the assumption that zones I, II, and III are associated with different ecological processes. Zone I is an area where *D. micans* has had the time to establish, and where factors affecting establishment and local population dynamics are assumed to exert an increased influence. Zone III is an area not yet colonized by the insect, where spatial factors associated with dispersal are assumed to be dominant. Zone II is a transition zone that presents intermediate values.

The positive correlation between attack density and plantation age can be interpreted mainly in relation to the beetle's relationship with its host tree. *Dendroctonus micans* is the largest European bark beetle (6–8 mm) and, because of its size, development of brood chambers requires a minimal bark thickness. As a consequence, it is generally considered that bark thickness determines the age at which a tree becomes susceptible (Grégoire 1988). The average age of the stands in this study was 26 years and ranged from 10 to 80 years. Although young trees may present local zones of high bark thickness (e.g., bottom of forks, or the bases of stems), older trees have a much larger bark area with suitable thickness for development of *D. micans* larvae through to maturity. Stands with older trees may thus potentially host larger populations and, consequently, favour faster population growth.

Increases in altitude are correlated with lower attack densities. A similar trend has been observed in northern North America where susceptibility of spruce stands to attack by *Dendroctonus rufipennis* is negatively associated with altitude in spruce forests in northern North America (Safranyik 1985). Tree vitality or resistance could be higher at higher altitudes; on the other hand, the lower temperatures at high altitude could also have direct effects on *D. micans* population dynamics. Firstly, low temperature is always associated with slower metabolism in insects, and to longer life cycles

in the particular case of *D. micans*. Its life cycle lasts approximately 1 year in warm countries such as Turkey (Serez 1979), up to 3 years in Scandinavian countries (Lekander et al. 1977), and is of intermediate lengths of 1–2 years in Belgium (Grégoire and Merlin 1984) and the U.K. (King and Fielding 1989), depending on dates of egg laying and climatic conditions. Attacked stands at low altitudes may support more generations over the same time period than others located higher up and, thus, suffer from a higher attack density. Secondly, *D. micans* adults require a temperature threshold of 21–23°C to take flight (Vouland et al. 1984), which is likely to be encountered less frequently at higher altitudes. Natural dispersal of *D. micans* may thus be favoured at low altitudes, and could increase the likelihood of colonization of nonattacked stands. Comparison of zone I and zone III with respect to these factors, indicates that, firstly, attack densities are not significantly correlated with altitude in zone III in a multiple regression framework and, secondly, that the correlation between attack density and plantation year is weaker in zone III (as measured by the effect estimate). These two results support the hypothesis that attack density in zone I is affected predominantly by factors affecting establishment and population dynamics.

In terms of spruce cover structure, high attack densities are correlated with a high shape index and with high numbers of small patches in the neighbourhood. Conversely, low attack densities are correlated with simple shapes surrounded by few large spruce patches. The role played by the shape index is probably the easiest to interpret, because a higher index is associated with a relatively greater length of forest edge to be encountered first by pioneer beetles dispersing from infested forests. Edges are also known to have different ecological characteristics compared with core habitats (Wiens et al. 1985; Turner 1989). Edge effect is usually organism-dependent in landscape ecological studies, so that some species have an affinity for edges, some are unaffected, and others are adversely affected (McGarigal and Marks 1995). *Dendroctonus micans* has been observed to favour stand edges (Granet and Perrot 1977) but it is not clear whether it is because edges are the first point of contact for arriving pioneer beetles, or because edges present local conditions potentially favoured by the insect (higher exposure to the sun, higher temperatures, or a higher amount of tree wounding). If it is assumed that zone III is an area where spatial effects are dominant, the fact that the relationship between MSI and attack density is only significant in zone III tends to favour the hypothesis that patches with a high shape index are likely to intercept more insects.

In a landscape-ecology context, patch density may affect a variety of processes. Patch density is a standardized measure of patch number, which is known to alter the dynamic of species interactions for predator-prey and competitive systems as has been shown in recent theoretical and modelling studies (Tilman and Kareiva 1997). This is unlikely to be the case during the period analysed here, because *D. micans*' main predator, *Rhizophagus grandis*, was not present in the United Kingdom at the time of the study, and because *D. micans* is protected from direct subcortical competitors (Grégoire 1988) by an extremely high tolerance to the host tree chemical defences (Everaerts et al. 1988). The number of patches may also determine the number of subpopulations

of *D. micans*, which may itself influence the dynamics and persistence of metapopulations. Metapopulation dynamics is based on the assumption that populations build up in isolated habitats as a result of migration and may become extinct as a consequence of resource utilization, habitat, or climatic changes (Hanski and Gilpin 1997). However, once successfully established in a spruce stand, it is unlikely that *D. micans* would become extinct, because the habitat in the present study was fairly stable, and was free of specific natural enemies and competitors. Furthermore, metapopulation dynamics assume fairly low levels of inter-patch migration, and *D. micans* is assumed to actively leave stands where it develops (Gilbert et al. 2001). It is thus unlikely that *D. micans* could have presented such metapopulation dynamics. Finally, high patch density reduces inter-patch distances, and this could positively influence *D. micans* dispersal by providing a network of relay habitats separated by shorter distances more easily covered by flying individuals. This interpretation could certainly be used in zone III, where attack density is related to patch density within a large 9-km buffer distance. However, it does not provide a convincing interpretation of the relationships observed in zone I, where attack density is related to patch density within a 1-km neighbourhood, a distance easily covered by flight. Interpretation of this effect in this neighbourhood may be closely related to the effect of mean patch area (MPAR1) also found significant for the same neighbourhood size. If the spruce area in a given neighbourhood is kept constant, a higher patch density translates into a smaller average patch area, and vice-versa. Both variables (PD1 and MAP1) that were significant in zone I thus represent the inverse extremes of the same relationship; attack density is higher when patches in the close neighbourhood (1 km) are small and numerous. Individual insects emerging from trees located in small patches quickly meet the stand edge and have the opportunity to leave and colonize other stands. Conversely, insects emerging in the middle of large stands do not need to move long distances, either by flight or walking, before encountering suitable breeding resources. Indeed, a large dense stand with closed canopy may have local climatic conditions, such as lower temperatures in the shaded conditions within a stand that would tend to preclude flight. Additionally, beetles may be prompted to leave the stand when their population level has reached the carrying capacity of the stand, which is likely to be reached more rapidly in small stands than in larger ones. The ratio between numbers of adult *D. micans* leaving and staying in a stand may thus be higher in small stands and explain why stands surrounded by numerous small patches were observed to have higher attack densities in zone I.

Spatial models of covariance of the multiple regression models indicated some spatial structure in the attacked-tree density after spatial trend removal, and range distance was varying over the three zones between 4.3 km in zone I and 7.2 km in zone III. In the period since 1984, the Forestry Commission has operated a peripheral survey and management zone that separates the colonized area from the rest of the United Kingdom, to minimize the amount of natural spread of *D. micans* to other parts of the country (Fielding et al. 1991). The concept of the peripheral zone is that it marks a 10-km-wide area outside the infested area, known to be

free of infestation. However, because of the natural spread of *D. micans*, annual surveys of all spruce within the protected zone are carried out, and all infested trees found are felled, and the immediate area is inoculated with *R. grandis* (O'Neill and Evans 1999). These survey data yielded a maximum natural dispersal rate of approximately 5–6 km/year (O'Neill and Evans 1999). It is very tempting to relate this observation to the observed spatial structure range of 4–7 km in the models developed here. However, the range of spatial dependence could not be used as such to estimate dispersal ability. Firstly, because it may incorporate spatial structure in which the explanatory factors are unknown (although this risk was reduced by analysing spatial structure of residuals) and, secondly, because the observed spatial dependence may be the consequence of many subsequent years of spread. Nevertheless, the measure of spatial dependence does allow quantification of the spatial scale at which dispersal occurs. The spatial structure was found to be strongest and with the longest range in zone III, lower with a lower range in zone II, and lowest with the shortest range in zone I. This tends to confirm the hypothesis that zone III is an area where spatial effects are dominant relative to zone I where they are weaker.

Bringing together the range of factors discussed above, attack densities in zone I show a weaker and shorter spatial structure, a stronger relationship to planting year, a relationship with altitude, and are related to the numbers of patches located in the very close neighbourhood (1 km). All these elements support the hypothesis that zone I is an area where attack density is mostly related to factors affecting population establishment and growth. Conversely, the idea that attack density in zone III is less dependent on stand and site conditions and more closely related to dispersal is supported by the stronger observed spatial dependence over a longer range. The factors are the positive relationship with the shape index (as a measure of detection of fragmented resources by flying pioneer beetles), the positive relationship with patch density within a long-distance neighbourhood, a weaker relationship to plantation year, and no relationship with altitude.

These results in themselves are not surprising. It is possible that, within the colonized area (zone I), all spruce stands could have been reached by *D. micans*, and that the observed variability depended on how well the beetles actually developed in different stands. It is also clear that the level of attack of stands located outside zone I depends mostly on whether a single female has managed to reach the stands or not. However, quantification of these assumptions is not trivial and is only made possible by the explicit incorporation of space in the analysis and modelling of these large-scale data. It also stresses the need for taking account of knowledge on large-scale gradients when analysing ecological systems at smaller scales.

The correlations and spatial models used in this study characterize only some aspects of the spatial ecology of *D. micans* in Britain, and it is likely that other factors, particularly other landscape characteristics, could play a role in explaining the spatial pattern of attack densities. Moreover, the impact of the factors found significantly correlated with attack density could only be fully demonstrated by separate experimental studies, especially if these factors are to be

used in an applied perspective. This study does, however, provide the first quantitative evidence that the spatial distribution of *D. micans* can be modelled at a regional scale, using site and stand conditions and landscape characteristics, and that the ecological processes affecting attack densities depend on the locations of stands relative to the main infested area. Further work stemming from these results could be considered, such as the analysis of sawmill locations and their main roads of access. Another approach could be to analyse in more details the spatio-temporal dynamics of the observed attacks within the Forestry Commission peripheral survey zone, where quantitative observations of attacked trees are recorded every year and, thus, provide a measure of natural spread relative to available spruce within the zone. Validation of the results presented here, as well as complementary experimental studies would be useful in an applied perspective in which the design of a GIS-based decision-support utility to be used in an integrated pest management programme would be a particularly attractive outcome, potentially applicable to all areas where *D. micans* is still expanding its range.

## Acknowledgements

The project was partly financed by the Fonds de la Recherche fondamentale collective (FRFC grants 2.4532.97 and 2.4578.99). Critical comments by anonymous reviewers are gratefully acknowledged.

## References

- Clifford, P., Richardson, S., and Hémon, D. 1989. Assessing the significance of the correlation between two spatial processes. *Biometrics*, **4**: 123–145.
- Cressie, N.A.C. 1993. *Statistics for spatial data*. John Wiley & Sons, New York.
- Dolmans, M., and Grégoire, J.-C. 1992. Utilisation d'un système d'information géographique (SIG) pour la gestion des populations de *Dendroctonus micans* (Kug.) (Coleoptera, Scolytidae) dans le sud du Massif Central. *Mém. Soc. R. Belge Entomol.* **35**: 517–521.
- Elkie, P., Rempel, R., and Carr, A. 1999. *Patch analyst user's manual*. Ontario Ministry of Natural Resources Northwest Science and Technology, Thunder Bay, Ont.
- Everaerts, C., Grégoire, J.-C., and Merlin, J. 1988. The toxicity of norway spruce monoterpenes to two bark beetle species and their associates. In *Mechanisms of woody plant defenses against insects*. Springer Verlag, New York. pp. 335–344.
- Fielding, N.J., Evans, H.F., Williams, J., and Evans, B. 1991. Distribution and spread of the great European spruce bark beetle, *Dendroctonus micans*, in Britain — 1982 to 1989. *Forestry*, **64**: 345–358.
- Forsse, E. 1989. Flight duration of eleven species of bark beetles (Scolytidae) and observations of aerial height distribution. Ph.D. thesis, Swedish Agricultural University, Uppsala, Sweden.
- Gilbert, M., and Grégoire, J.-C. 2003. Site condition and predation influence a bark beetle's success: a spatially realistic approach. *Agric. For. Entomol.* **5**. In press.
- Gilbert, M., Vouland, G., and Grégoire, J.-C. 2001. Past attacks influence host selection by the solitary bark beetle *Dendroctonus micans*. *Ecol. Entomol.* **26**: 133–142.
- Granet, A.M., and Perrot, J.M. 1977. *Dendroctonus micans* Kug. dans le sud-est du Massif central. Aires d'extension et premier essai d'interprétation des dommages. Mémoire de 3<sup>e</sup> année, École Nationale des Ingénieurs des Travaux des Eaux et Forêts, Nancy, France.
- Grégoire, J.-C. 1988. The greater European spruce beetle. In *Dynamics of forest insect populations: patterns, causes, implications*. Plenum Press, New York. pp. 455–478.
- Grégoire, J.-C., and Merlin, J. 1984. *Dendroctonus micans* in Belgium: the situation today. In *Proceedings of the EEC Seminar, Biological Control of Bark Beetles, Dendroctonus micans*, 3–4 Oct. 1984, Brussels, Belgium. Edited by J.-C. Grégoire and J.M. Pasteels. Commission of the European Communities, Brussels, Belgium. pp. 48–62.
- Gumpertz, M.L., Wu, C.-T., and Pye, J.M. 2000. Logistic regression for southern pine beetle outbreaks with spatial and temporal autocorrelation. *For. Sci.* **46**: 95–107.
- Hanski, I., and Gilpin, M.E. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, Calif.
- Hengeveld, R. 1989. *Dynamics of biological invasions*. Chapman and Hall, London.
- Isaaks, E.H., and Srivastava, R.M. 1989. *An introduction to applied geostatistics*. Oxford University Press, Oxford, U.K.
- Keitt, T.H., Bjornstad, O.N., Dixon, P.M., and Citron-Pousty, S. 2002. Accounting for spatial pattern when modeling organism–environment interactions. *Ecography*, **25**: 616–625.
- King, C.J., and Fielding, N.J. 1989. *Dendroctonus micans* in Britain — its biology and control. *For. Com. Bull.* **85**: 1–11.
- Lekander, B., Bejer-Petersen, B., Kangas, E., and Bakke, A. 1977. The distribution of bark-beetles (Coleoptera, Scolytidae) in the Nordic Countries. *Acta Entomol. Fenn.* **32**: 1–100.
- Lennon, J.J. 2000. Red-shifts and red herrings in geographical ecology. *Ecography*, **23**: 101–113.
- Liebold, A.M., Elmes, G.A., Halverson, J.A., and Quimby, J. 1994. Landscape characterization of forest susceptibility to gypsy moth defoliations. *For. Sci.* **40**: 18–29.
- Little, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.D. 1996. *SAS System for mixed models*. SAS Institute Inc., Cary, N.C.
- McGarigal, K., and Marks, B.J. 1995. *FRAGSTATS: spatial pattern analysis program for quantifying landscape structure*. Reference manual. Forest Science Department, Oregon State University, Corvallis, Ore.
- O'Neill, M., and Evans, H.F. 1999. Cost–effectiveness analysis of options within an integrated crop management regime against great spruce bark beetle, *Dendroctonus micans* Kug. (Coleoptera: Scolytidae). *Agric. For. Entomol.* **1**: 151–156.
- O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zymunt, B., Christensen, S.W., Dale, V.H., and Graham, R.L. 1988. Indices of landscape pattern. *Landsc. Ecol.* **1**: 153–162.
- Pannatier, Y. 1996. *VARIOWIN: software for spatial data analysis in 2D*. Springer-Verlag, New York.
- Riitters, K.H., O'Neill, R.V., Hunsaker, C.T., Wickham, J.D., Yankee, D.H., Timmins, S.P., Jones, K.B., and Jackson, B.L. 1995. A factor analysis of landscape pattern and structure metrics. *Landsc. Ecol.* **10**: 23–40.
- Rossi, R.E., Mulla, D.J., Journel, A.G., and Franz, E.H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecol. Monogr.* **62**: 277–314.
- Safranyik, L. 1985. Infestation incidence and mortality in white spruce stands by *Dendroctonus rufipennis* Kirby (Coleoptera, Scolytidae) in central British Columbia. *J. Appl. Entomol.* **99**: 86–93.

- Serez, M. 1979. Der Riesenbastkaefer (*Dendroctonus micans* Kug.) in der Turkei (Coleoptera: Scolytidae). Turk. Bitki Koruma Derg. **3**: 17–24.
- Sharov, A.A., Liebhold, A.M., and Roberts, E.A. 1997. Correlation of counts of gypsy moth (Lepidoptera: Lymantriidae) in pheromone traps with landscape characteristics. For. Sci. **43**: 483–490.
- Shigesada, N., and Kawasaki, K. 1997. Biological invasions: theory and practices. Oxford University Press, Oxford, U.K.
- Taylor, L.R. 1961. Aggregation, the variance and the mean. Nature (London), **189**: 732–735.
- Tilman, D., and Kareiva, P. 1997. Space ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, N.J.
- Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. **20**: 171–197.
- Vouland, G., Giraud, M., and Schvester, D. 1984. The teneral period and the flight-taking in *Dendroctonus micans* Kug. (Coleoptera: Scolytidae). In Proceedings of the EEC Seminar, Biological Control of Bark Beetles, *Dendroctonus micans*, 3–4 Oct. 1984, Brussels, Belgium. Edited by J.-C. Grégoire and J.M. Pasteels. Commission of the European Communities, Brussels, Belgium. pp. 68–79.
- Wiens, J.A., Crawford, C.S., and Gosz, J.R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos, **45**: 421–427.