

## Past attacks influence host selection by the solitary bark beetle *Dendroctonus micans*

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**Abstract.** 1. A spatio-temporal study of host selection and local spread of a solitary bark beetle attacking live spruce *Dendroctonus micans* (Kugelann) was carried out using a combination of standard statistical methods, geostatistical analyses, and modelling. The study was based on data from three plots (150–300 trees, 0.3–1 ha) from 1978 to 1993. All trees were mapped and successful and abortive bark-beetle attacks on each tree were counted annually. Because the attacked trees usually survived, temporal attack patterns as well as spatial patterns could be analysed.

2. The distribution of successful insect attacks on the trees was slightly aggregative, indicating some degree of choice rather than totally random establishment.

3. The level of yearly individual attacks per tree was very stable, suggesting that *D. micans* usually leave the host in which they develop.

4. The attacked trees were distributed randomly in the plots; at the study's spatial scale, the insects dispersed freely throughout the plot (no spatial dependence).

5. On the other hand, time dependence was strong; some trees were attacked repeatedly while others were left untouched.

6. Among a choice of scenarios (random attack, fixed variability in individual host susceptibility, induced host susceptibility following random attack), the best fit was obtained with the model involving induced individual host susceptibility. This type of relation to the host tree contrasts strongly with patterns generally described in host–plant relationships (including gregarious, tree-killing bark beetles), where local herbivore damage results in induced resistance.

7. These results suggest that the first attacks in a new stand are made at random, that all or most of the beetles emerging from a tree disperse and resample the stand, and that they settle preferentially on trees that were colonised successfully by previous generations.

**Key words.** *Dendroctonus micans*, dispersal, geostatistics, insect host–tree relationship, Scolytidae, tree susceptibility.

### Introduction

For most primary bark-beetle species, successful establishment on a host tree requires pheromone-mediated mass attack and

inoculation of fungal pathogens to overcome the tree's defences (Coulson, 1979; Wood, 1982). Convergent evidence suggests that the pioneer beetles responsible for initiating mass attack land on the trees at random and subsequently make their choice at very close range using olfactory or gustatory clues (Raffa & Berryman, 1980; Moeck *et al.*, 1981).

Contrasting with these species, *Dendroctonus micans* (Kugelann) is a solitary coloniser of live spruce, which is not

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associated with fungal pathogens (Lieutier *et al.*, 1992), does not use aggregation pheromones, and manages to co-exist with the living host (Grégoire, 1988) during its whole life cycle. This more parasitic way of life relies on a high level of resistance to the monoterpenes that constitute the tree's constitutive defences (Everaerts *et al.*, 1988).

Each single *D. micans* female, fertilised in the natal brood chamber, thus has to find a host tree on its own. How it does this has so far remained largely unexplored. *Dendroctonus micans* appears sensitive to host odours (Vasechko, 1978; Tømmerås, 1989) and has been reported to concentrate on stand edges and on wounded or forked stems (e.g. Granet & Perrot, 1977) or on trees attacked by pathogenic fungi such as *Heterobasidion annosum* (Brefeld) (Francke-Grosman, 1954). More anecdotal evidence suggests that *D. micans* spreads from one tree to neighbouring trees (e.g. Quairière, 1905).

The aim of the study reported here was to determine whether *D. micans* colonises trees at random or whether distinct patterns (spatial proximity, individual tree resistance or susceptibility) govern this choice. This study of *D. micans*' spatio-temporal distribution at the stand level was facilitated by the fact that most of the attacked trees can survive through many generations of the beetle. Comparisons could thus be made across successive years in the same stands and on the same trees. For this purpose, a large data set built up by the Institut National de la Recherche Agronomique at Avignon (France) from a number of permanent plots of 150–300 trees established throughout the French Massif Central between 1978 and 1993 was used.

## Material and methods

### Study plots and data collection

Three plots situated in different areas of the southern Massif Central were used in the study: Le Bleymard (State forest of Le Goulet, Lozère, 44°32'N, 03°45'E), Le Bougès (State Forest of Le Bougès, Lozère, 44°21'N, 03°44'E), and Le Mézenc (State forest of Le Mézenc, Haute-Loire, 44°54'N, 04°09'E) (Table 1, Fig. 1). Each of the plots was part of a wider spruce stand. During surveys conducted in the autumn of each year, every *D. micans* attack under 2 m on every tree in the plots was recorded, distinguishing between successful and abortive attempts. The symptoms used for this purpose were the resin tubes produced by boring beetles, which vary in shape and colour according to the insects' success. The resin tubes

resulting from abortive attacks are usually lighter in colour because they contain more resin than frass; this high resin content also gives them a poorly structured, drooping shape. A group of resin tubes very close together usually corresponds to one single attack with multiple attempts to enter the bark; such groups were counted as one attack. Above 2 m, a ranking scale (from 0 to 3) was used to describe insect activity (Vouland, 1991). These data were entered into a database (MS Excel) and mapped using a GIS vectorial database [Arc/Info version 7(ESRI)] for further spatial analysis.

The population dynamics of *Dendroctonus micans* differed markedly among the three stands (Fig. 2). At Le Bleymard, the first attacks occurred in 1978. The proportion of attacked trees increased steeply in 1983 and, after a lapse in 1986–87, continued to increase to reach a maximum in 1990. At Le Bougès, the proportion of attacked trees showed one main period of increase between 1985 and 1993, with a peak in 1988. At Le Mézenc, the first attacks occurred in 1981; the percentage of attacked trees increased slowly until 1989, then grew more steeply to reach a maximum in 1992.

The predator, *Rhizophagus grandis* (Gyllenhal) (Coleoptera, Rhizophagidae), was present in all plots, however it was introduced several years after the study plots had been established and remained uncommon for several years after its introduction. For example, in Le Mézenc, after a release in 1987, it was still rare in 1993 (Van averbeke & Grégoire, 1995). Furthermore, although *R. grandis* certainly influenced the population dynamics of *D. micans* in some stands, it probably had no impact on bark beetle dispersal because it only attacks immature stages.

### Choice of a data set

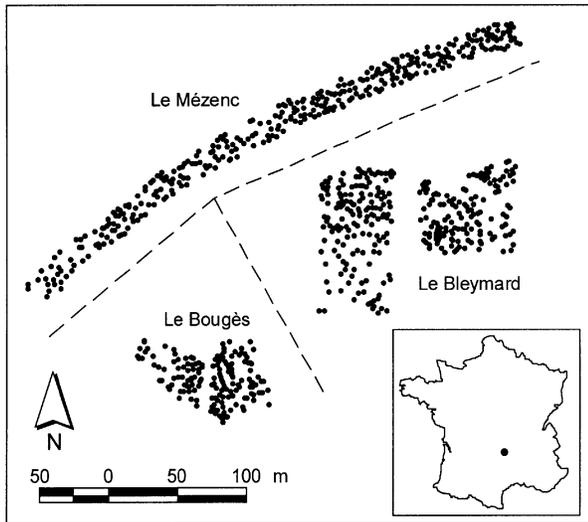
In order to increase the accuracy of the study, it was decided to use only the truly quantitative data on successive attacks and recorded below 2 m. A first series of analyses was therefore made to determine whether the attacks up to this level gave a good reflection of the total attacks on each tree, i.e. whether they constituted a large and constant proportion of the attacks in the plots.

### Patterns of individual tree colonisation

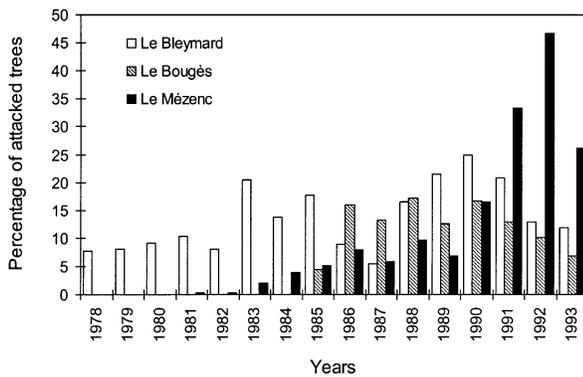
The relationship between the intensity of attacks in the stand (i.e. the proportion of attacked trees) and the intensity of attacks per attacked tree (i.e. the average number of attacks per attacked

**Table 1.** Characteristics of the study plots.

Stand	Planting date	Density (trees per ha)	Altitude (m)	Slope (°)	Aspect	Number of trees at start
Le Bleymard	1911	320	1400	10	N-E	309
Le Bougès	1921	450	1090	5	N	159
Le Mézenc	1906	380	1510	7	N-E	337



**Fig. 1.** Maps of the study plots. Each dot indicates the location of a tree. All plots are represented at the same scale and orientation but are actually separated by more than 20 km.



**Fig. 2.** Percentage of attacked trees in the three plots (1978–1993).

tree) was analysed each year for each stand by comparing the observed distribution of attacks per attacked tree with a random pattern of tree colonisation where each new beetle entering the stand had an equal probability of settling on any tree. A binomial model was used where each insect entering the stand constituted an independent trial and where any tree had a probability of being attacked  $p = 1/T$ ,  $T$  being the total number of trees. The total number of trials was established by summing all successful attacks under 2 m recorded in the surveys each year for each stand. The standardised Morisita's index (Morisita, 1962; see below) was also used to estimate whether the distribution of insects on trees (each tree being a sample unit) was regular, random, or clumped.

#### *Spatial patterns of tree colonisation in the stands*

Quadrat analysis (Southwood, 1996) was performed to analyse the spatial distribution of attacked trees in each plot.

Quadrat counts were carried out using a raster GIS [GRID: Arc/Info version 7 raster module (ESRI)]. Numbers of attacked trees were recorded within adjacent square windows covering the study plot areas. Successive increasing window sizes were employed ( $6 \times 3$ ,  $6 \times 6$ ,  $12 \times 6$ ,  $12 \times 12$ ,  $24 \times 12$  and  $24 \times 24$  m). Standardised Morisita's indices were computed for the different years and quadrat sizes. This index was described by Myers (1978) as one of the best dispersion indices because of its independence of population density and sample size.

The Morisita's index of dispersion is defined by the following equation where  $x$  represents quadrat counts (Morisita, 1962):

$$I_d = n \frac{\sum(x^2) - \sum x}{(\sum x)^2 - \sum x}$$

The value  $I_d(\sum x - 1) + n - \sum x$ , where  $I_d$  is the Morisita's index,  $x$  is the quadrat count, and  $n$  is the number of quadrats, follows a  $\chi^2$  distribution with  $n - 1$  d.f. The standardised Morisita's index was set out by Smith-Gill (1975) to improve Morisita's index by putting it on an absolute scale that varies between  $-1$  and  $+1$ ; values  $< -0.5$  and  $> 0.5$  represent a significantly regular and clumped distribution respectively, with 95% probability.

Dispersion indices, however, focus on frequency distributions of samples but ignore their spatial location and therefore often fail to differentiate among different spatial patterns or structures (Jumars *et al.*, 1977). For this reason, spatial dependence in the insects' distribution was also studied using geostatistical techniques.

These geostatistical tools allow exploration and quantification of the spatial continuity of a georeferenced data set. An excellent presentation of the use of such methods in applied ecology was given by Rossi *et al.* (1992); a more comprehensive approach was presented by Isaaks and Srivastava (1989), and extensive theoretical details were given by Cressie (1993). The principle of spatial continuity is based on the premise that pairs of random variables only short distances apart have values that are more similar than might be expected when compared with other pairs of the same variables that are further from each other (Isaaks & Srivastava, 1989). There are different tools in geostatistics to explore and quantify the spatial continuity of a data set. The most useful are h-scatterplots, variograms, nonergotic correlograms, and nonergotic covariance measures (Rossi *et al.*, 1992). Nonergotic correlograms were used in this study because they account for both the local mean and variance and hence are more suitable to reveal the underlying spatial continuity of data where the sample points are clustered. A nonergotic correlogram is a graph that summarises the value of the spatial autocorrelation coefficient for different increasing distance intervals (termed *lags*). Each spatial autocorrelation coefficient is a measure of the proportion of the total variance of the total sample that could be attributed to spatial dependence; in other words, it is a measure of the correlation between samples separated by the lag distance. In geostatistical context, the nonergotic correlogram is represented in a form where the ordinate is  $1 - \hat{\rho}(h)$  [ $\hat{\rho}(h)$  being the spatial auto-correlation coefficient], firstly

because the true semivariance and the true correlogram are, under stationarity conditions, related by the relation  $\gamma(h)\sigma^2 = 1 - \rho(h)$ , and secondly because it allows better comparison with other semivariance estimators. Typically, it is a rising curve [points a short distance apart have fairly similar values,  $1 - \hat{\rho}(h)$  is therefore low; while points further apart have less correlated values and a higher  $1 - \hat{\rho}(h)$  value] that levels off at a given lag known as the *range* (lag distance over which sample points are independent, with  $1 - \hat{\rho}(h)$  therefore equal to 1), while the height is known as the *sill*. Points separated by a null distance have a spatial autocorrelation coefficient of one, so the curve should start at the origin of the two axes. This is rarely the case with ecological data, and the correlogram value at which the model intercepts the y-axis is termed the *nugget*. The nugget may represent two sources of variability: the spatial variability at a scale smaller than the minimum lag distance and the experimental error. Nonergotic correlograms can also be used to identify statistical temporal dependence; in this case, time lags are used instead of distance lags and the nonergotic correlogram is a measure of the correlation among samples separated by increasing time period. The experimental nonergotic correlogram for separation vector  $h$  (distance or time) was calculated according to the following formula (Pannatier, 1996):

$$\hat{\rho}(h) = \frac{\hat{C}(h)}{s_{-h} \cdot s_{+h}}$$

where

$$\hat{C}(h) = \frac{1}{N(h)} \sum_{i=1}^{N(h)} v(x_i) \cdot v(x_i + h) - m_{-h} \cdot m_{+h}$$

$\hat{C}(h)$  is the estimator of the nonergotic covariance where  $v(x_i)$  and  $v(x_{i+h})$  are two data points separated by a vector  $h$  (the lag). Datum  $v(x_i)$  is the tail and  $v(x_{i+h})$  is the head of the vector,  $N(h)$  is the total number of data pairs separated by lag  $h$ ,  $m_{-h}$  and  $m_{+h}$  are the mean of the points that correspond to the tail and the head of the vector respectively, and  $s_{-h}$  and  $s_{+h}$  are the standard deviation of the tail values and head values of the vector respectively. XYZ files were generated from the GIS database and used to compute correlograms using VARIOWIN (Pannatier, 1996), a Windows-based program designed to perform exploratory variography. Nonergotic correlograms were calculated using the number of attacks on each tree each year in the three stands.

#### Temporal patterns of tree colonisation in the stands

Temporal patterns were studied using temporal correlograms to compute statistical time dependence for increasing time lags. The theory used to build up this estimator was the same as the spatial correlogram described above except that only one dimension (time) was used.

#### Susceptible and historical models

In addition to the binomial model used to test random tree colonisation in the stands (see Patterns of individual tree

colonisation), two other models were tested using Monte-Carlo simulations.

The hypothesis behind the first model (termed *susceptible* model hereafter) is that some trees present a higher probability of being attacked from the start and keep this probability for the whole period. In this model, some trees (Ns) are chosen randomly from the set of living trees and receive a higher probability of being attacked (Ps). Each insect entering the stand has a probability Ps of attacking susceptible trees and Pn of attacking normal trees. The model uses two inputs from the observed distributions (the number of attacks per year and the total number of trees) and two inputs established by hypothesis (the proportion of susceptible trees and the ratio Pn:Ps).

The hypothesis underlying the second model (termed *historical* model) is that all trees are equal at the start but that their probability of being attacked depends on whether they were attacked during the previous year. Every year, trees attacked the previous year are given a higher probability of being re-attacked (Pa) while those that were not attacked are given a lower probability (Pna). The model uses two inputs from the observed distributions (the number of attacks per year and the total number of trees) and one input established by hypothesis (the ratio Pa:Pna).

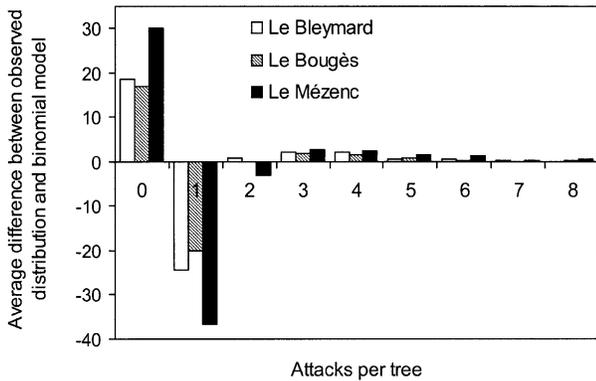
The simulations were carried out using a program designed specifically in Visual Basic 5. Monte-Carlo simulations were repeated 5000 times. In the susceptible model, simulations were repeated for various combinations of Ns (number of susceptible trees) and r (ratio Pn:Ps) until the best fit was found between the observed and simulated distribution. The same iterative process was used to identify the best ratio Pa:Pna of the historical simulation.

These models do not take into account the spatial location of host trees. Such a simplification was permitted by the total absence of statistical spatial dependence in insect counts on trees (see Results).

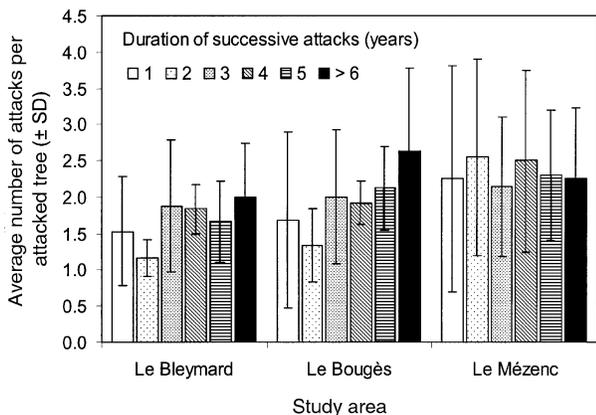
## Results

### Choice of a data set

Over the whole period of survey (1978–1993), the proportions of attacks up to 2 m represented an average 68% in Le Bleyard, 69% in Le Bougès, and 71% in Le Mézenc. These proportions remained stable in each of the three stands, as shown by the significant correlation over the three plots and the whole study period between the numbers of trees attacked up to 2 m and the total numbers of attacked trees ( $R^2 = 0.90$ ,  $P < 0.001$ , 38 d.f.). Moreover, the correlation over the whole period between the number of attacks below 2 m and the total number of attacks on each tree was significant and positive for the three plots (Le Bleyard:  $R^2 = 0.25$ ,  $P < 0.001$ , 783 d.f.; Le Bougès:  $R^2 = 0.35$ ,  $P < 0.001$ , 249 d.f.; Le Mézenc:  $R^2 = 0.46$ ,  $P < 0.001$ , 767 d.f.). The analyses were thus focused only on the data up to 2 m.



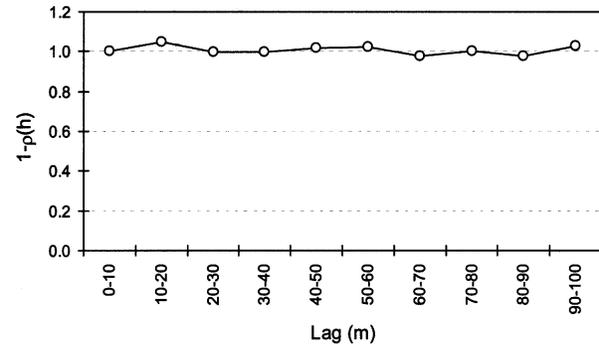
**Fig. 3.** Differences between the observed distribution of attacks per tree and the binomial distribution in Le Bleymard, Le Bougès, and Le Mézenc. The binomial model underpredicts numbers of unattacked trees and numbers of trees with three or more attacks, and overpredicts numbers of trees with only one attack. In the binomial model, there are more attacked trees than observed, but they bear fewer attacks, the total numbers of attacks in the plots being the same in both distributions.



**Fig. 4.** Average number of attacks per attacked tree for classes of trees that have been attacked successively over increasing periods. There is no significant increase in attack intensity for trees that have been attacked repetitively over successive years.

#### Patterns of individual tree colonisation

The frequency distribution of *observed* successful attacks per tree obtained by pooling the data from the three plots differed markedly from the distribution of *random* attacks generated by the binomial function (Fig. 3). The main difference between these two distributions was that there were many more unattacked trees in reality than in the random attack model, and more trees attacked only once in the random attack model than in reality. For attack densities higher than two attacks per tree, there were consistently more observed occurrences than predicted by the model. These results indicate an aggregative trend that was tested by fitting the observed attack density distribution to a negative binomial distribution.



**Fig. 5.** Nonergotic correlogram of the number of attacks per tree at Le Bleymard in 1992. This correlogram shows a *pure nugget effect*, indicating that the probability of a tree being attacked is statistically independent of its distance from any other tree in the plot.

The fitting, as measured by the  $\chi$  probability values, was good for most cases (32 of the 38  $\chi$  *P*-values were between 0.05 and 0.95). The standardised Morisita's index of dispersion was also computed as a complementary measure of gregariousness. All the measures obtained (all plots, all years) were higher than the limit value of 0.5, confirming this aggregative trend. Attack density per tree, however, was not dependent on the number of successive years during which the trees were attacked (Fig. 4).

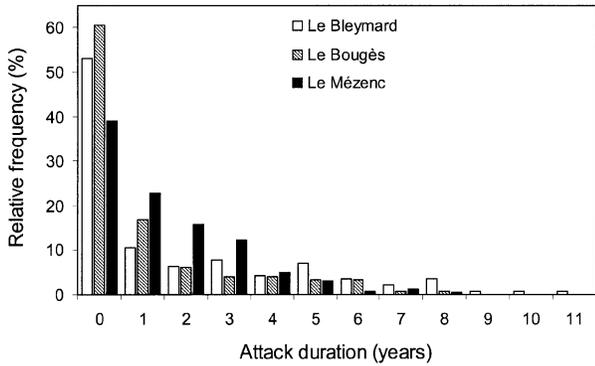
#### Spatial patterns of tree colonisation in the stands

The standardised Morisita's indices calculated on the basis of the quadrat counts of attacked trees ranged from  $-0.554$  to  $0.501$  over the three plots during the whole period of observation. They do not indicate a significantly clumped or regular spatial pattern of the attacked trees at the scale of this study. The attacked trees were distributed randomly, whatever the year or the window size.

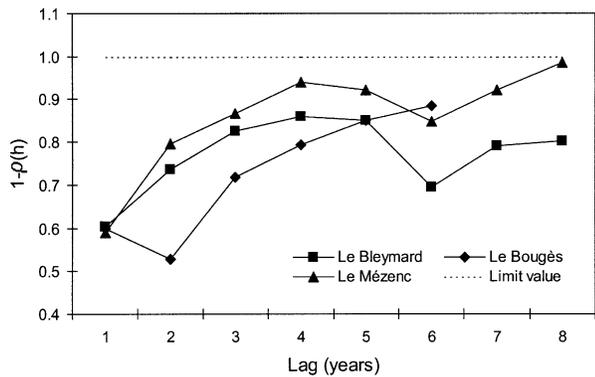
The nonergotic correlograms based on the numbers of attacks on each tree show *pure nugget effect* [i.e. a total absence of spatial autocorrelation among samples for all distance classes (lags),  $\rho=0$  for all lags (Isaaks & Srivastava, 1989)] for most years and plots (see, for example, Fig. 5 for Le Bleymard, 1992). In some other nonergotic correlograms, there were differences at the first lag (distance  $< 10$  m): the  $1 - \hat{\rho}(h)$  value in Le Bleymard was 0.853 in 1981, 0.878 in 1983, and 0.725 in 1991. It was 0.854 in 1987 in Le Bougès and 0.793 in 1986 in Le Mézenc. All the other values were  $> 0.9$  for the first lag and  $> 0.95$  for the other lags. The density of attacks per tree cannot therefore be attributed to spatial dependence from tree to tree. In the three stands and for the whole period considered, the number of insects on any tree was spatially independent of the number of insects on neighbouring trees.

#### Temporal patterns of tree colonisation in the stands

The distribution of attack duration on individual trees (Fig. 6) was not random. A  $\chi^2$  comparison test carried out



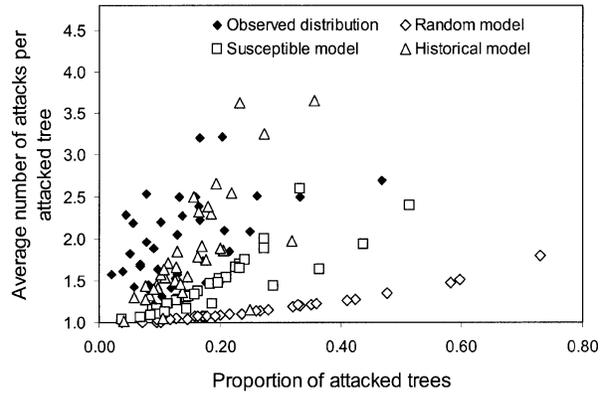
**Fig. 6.** Frequency distribution of the number of years during which individual trees were attacked over the study period.



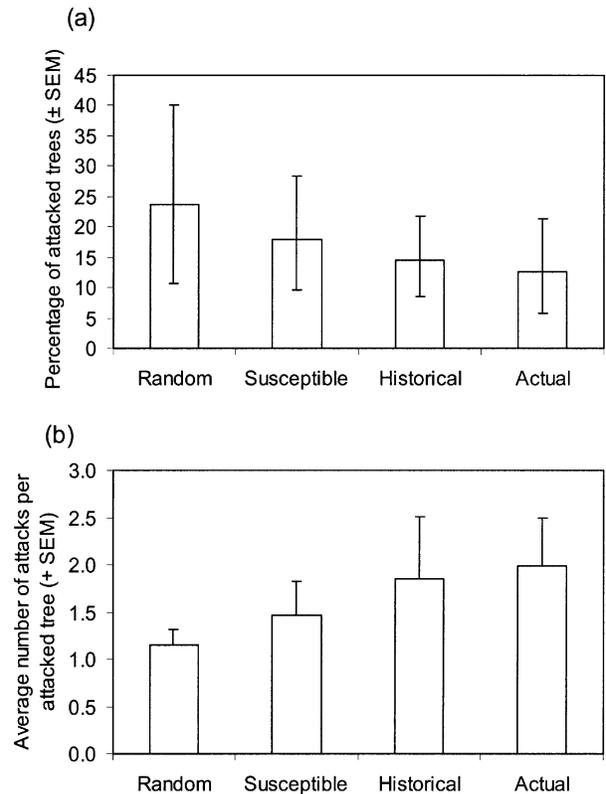
**Fig. 7.** Nonergotic time correlograms (lags are time periods instead of distances) of number of attacks per tree in the three plots showing a temporal structure (autocorrelation coefficient  $\rho=0.4$  in all plots for the first lag of 1 year). This indicates that the probability of a tree being attacked depends strongly on whether it was attacked in the previous year.

between the observed distributions and Poisson distributions for each site indicated highly significant differences (Le Bleybard:  $\chi^2=485.6$ ,  $P<0.001$ , d.f.=8; Le Bougès:  $\chi^2=175.2$ ,  $P<0.001$ , d.f.=8; Le Mézenc:  $\chi^2=1536$ ,  $P<0.001$ , d.f.=8). The main difference between the observed distributions and Poisson distributions was the very large number of trees that remained unattacked over the whole period; correlatively, there were more trees that remained attacked over a long period than expected from the Poisson distributions. This characteristic is less obvious in Le Mézenc.

Time correlograms (Fig. 7) showed a strong statistical dependence of the attacks on each tree in the three plots. In the three sites, 40% of the total variance from one year to the next (as indicated by autocorrelation coefficient  $\rho=0.4$  in all plots for the first lag of 1 year) can be modelled as temporal dependence (Rossi *et al.*, 1992). Except for Le Bougès, time dependence decreased for higher lags, reaching a sill for lags  $\leq 4$  years. At Le Mézenc, there was no more time dependence for lags  $>7$  years.



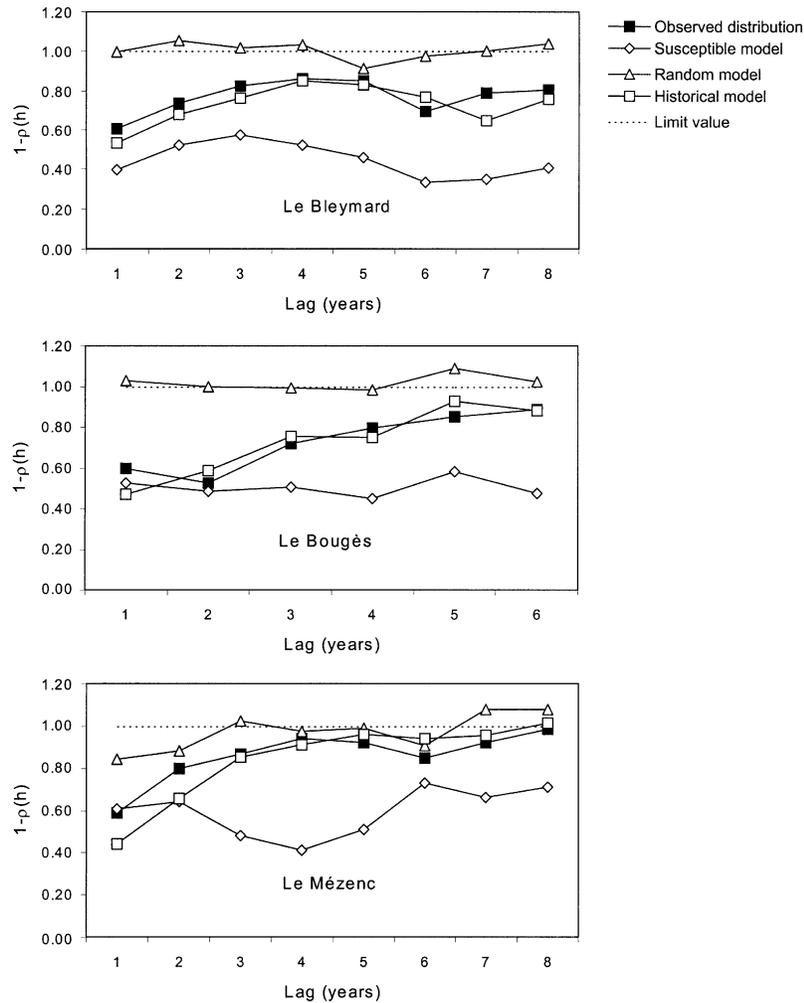
**Fig. 8.** Relationship between observed proportions of attacked trees in the plots and numbers of attacks per tree either observed or predicted by three different models.



**Fig. 9.** (a) Average proportions of attacked trees: observed and predicted by the three models. (b) Average numbers of attacks per attacked tree: observed and predicted.

*Susceptible and historical models*

Attack patterns per tree obtained by the random (positive binomial), susceptible, and historical models are shown in Fig. 8. The best parameters found iteratively for the susceptible model were: Le Bleybard:  $P_s:P_n=21$ ,  $N_s:N=23\%$  (ratio between the number of trees set as susceptible and the total



**Fig. 10.** Nonergodic time correlogram of observed and predicted numbers of attacks per trees in the three plots showing a pure nugget effect for the random model, a strong and constant temporal dependence for the *susceptible* model, and a good fit between the observed values and those predicted by the *historical* model.

number of trees); Le Bougès: Ps:Pn = 21, Ns:N = 26%; Le Mézenc: Ps:Pn = 10, Ns:N = 40.5%. The best parameters of the historical model were: Le Bleymard: Pa:Pna = 45.25; Le Bougès: Pa:Pna = 39.5; Le Mézenc: Pa:Pna = 34.5. The historical model clearly provides the best results with a distribution very close to the observed data. The susceptible model showed intermediate results while the random model diverged strongly from the observed distribution. These results were tested using a one-way ANOVA comparing averages of transformed (angular transformation) percentages of attacked trees of observed and modelled distributions (Fig. 9). A similar test was carried out on the average number of attacks per attacked tree (Fig. 9). The mean difference between percentages of attacked trees was highest for the random model ( $P < 0.001$ ), lower for the susceptible model ( $P < 0.05$ ), and lowest for the historical model ( $P = \text{NS}$ ). Similarly, the mean difference between numbers of attacks per attacked trees was highest for the random model ( $P < 0.001$ ), lower but still highly significant for

the susceptible model ( $P < 0.001$ ), and lowest for the historical model ( $P = \text{NS}$ ).

Temporal correlograms based on distributions generated by the random, susceptible, and historical models are presented in Fig. 10. As expected, the random distribution showed a correlogram with a pure nugget effect, indicating no time dependence. The susceptible distribution showed a flat correlogram presenting constant time dependence over the time lags. The historical distribution presented correlograms similar to those of the observed distribution, confirming the validity of the historical model.

## Discussion

The general picture that appears at the scale of this study is that *D. micans* usually leave the trees where they have developed, disperse freely throughout the stand, and preferentially

colonise hosts that have been attacked previously. This process differs radically from the host colonisation patterns of other primary bark beetles in several important ways: (1) each individual has to go through the whole process of host selection as there is no aggregation pheromone to signal susceptible trees; (2) the host seems to develop induced susceptibility instead of induced resistance as described for other primary bark beetles (Paine *et al.*, 1997); (3) intra-specific competition seems minimal, first because of the lack of aggregation pheromones and second because of an unknown mechanism stabilising the numbers of broods per tree. Further attention will be given below to these different points.

The comparison of observed data and binomial model shows that fewer trees are attacked in the stands than expected from a truly random process, indicating a trend for insects to aggregate on some trees. Because adults do not produce aggregation pheromones, this aggregative attack pattern reflects active host-selection processes by each individual beetle. Two hypotheses might explain this pattern. (1) Some degree of clumping of the attacks on trees might be related to a tendency in emerging insects to remain on the tree of origin. This has been observed for example by Francke-Grossmann (1949), who described young females starting new egg galleries from inside the brood chamber in which they developed (such attacks were not taken into account in the present study because counts were based on resin tubes produced by boring beetles). Istrate (1972) observed emergent insects taking off from a tree then flying back. In laboratory conditions, each single female is able to produce an average of 150 young adults (Grégoire & Merlin, 1984); in the field, broods of  $\approx 100$  individuals are commonly found (J.-C. Grégoire, unpublished). Unless very high mortality occurs during development and establishment, such a cumulative process should therefore result in a steep increase in attacks per tree, which does not appear in the records. Indeed, as shown in Fig. 4, trees attacked for many years in a row do not bear more attacks than trees attacked for a shorter period. Most of the beetles are thus definitely leaving their natal trees. (2) Nonrandom choice of host tree could be due to the dispersal behaviour of *D. micans*. Although detailed information is lacking, the bark beetle appears to be a rather clumsy flyer, with a high take-off temperature threshold of 21 °C (Vouland *et al.*, 1984), and there is a possibility that at least in some particularly cool years, it might be able to just glide or even walk from tree to tree. Tree colonisation could be a slow diffusion process from tree to neighbouring trees. An aggregated spatial distribution of attacked trees would then reflect this behaviour. This hypothesis clearly does not fit with the results of the quadrat analyses and correlograms. There is no spatial dependence or spatial aggregative pattern in tree colonisation at the scale of the study, i.e. within a 150 m radius.

These results do not mean that, in absolute terms, *D. micans*' spatial dispersal is completely random or spatially independent of site or stand condition. Their validity is probably restricted to the spatial scale of the study. The plots, with their reduced size, present homogeneous site and stand characteristics, and the insect's flight ability is probably higher than previously

thought, exceeding the size of the plots and allowing the beetles free choice of host within the plot.

Theoretical studies based on cellular automata models (Tilman *et al.*, 1997) provide support for this hypothesis. They have shown that dispersal in a purely homogeneous habitat may exhibit strong spatial patterns as long as dispersal range is small compared with the scale of study. Conversely, when dispersal exceeds the study scale, the spatial distribution of colonised sites appears to be random. This is probably what was observed here. At a larger scale, exceeding flight range and allowing heterogeneity in site and stand conditions, however, spatial effects are likely to exert an increasing influence. Studies concentrating on larger stands should provide further insight in this respect.

These results suggest that nonrandom choice of host trees is probably caused by nonspatial factors related to the trees themselves. They show that trees are attacked more repetitively than expected from a random process (Fig. 6) and reveal a strong temporal dependence of the insect counts on trees (Fig. 7).

Two hypotheses have been explored: these tree-related factors can either pre-exist the insects' attacks or arise from the insects' activity. The first hypothesis is supported by many reports of particular trees (forked stems, trees wounded or infected by fungi) being favoured by the insects. These trees could accumulate insects that could have been arrested after random landing or attracted by visual or chemical clues. On the other hand, a proportion of the trees could be protected against *D. micans*. There is some evidence of individual tree resistance to *D. micans* caused by physical or chemical factors: resin (Grégoire, 1985), lignin (Wainhouse *et al.*, 1990), or stilbenes (Storer & Speight, 1996).

This scenario does not, however, accord well with the simulations, where the historical model generated the best fit with the observed data. How could previous attacks affect host resistance, susceptibility, or attractiveness?

One possibility is that brood chambers release compounds attractive to *D. micans*, either primary attractants (Vasechko, 1978) or volatiles produced by the beetles' activity. In a field experiment designed to compare the numbers of insects landing on attacked and nonattacked trees, however, no significant attractivity of attacked trees could be detected (J.-C. Grégoire *et al.*, in prep.).

Another possibility is that tree susceptibility is induced by previous attacks. Brood chambers intersecting resin ducts could drain them, and the vicinity of these chambers could therefore provide safer spots for further insect establishment. During a recent field experiment (M. Gilbert *et al.*, in prep.), in which 50 attacked spruces were felled and analysed, it was found that 85% of the attacks were distributed vertically on one-quarter of the trunk, with no absolute preferred compass orientation, suggesting that the insects attacked areas above and under previous attacks preferentially. Other authors have analysed how wounding could influence *D. micans*' attacks. Lieutier *et al.* (1992) showed that attacks had a higher rate of success between or under artificial wounds. Storer and Speight (1996) found changes in bark characteristics around and under artificial wounding as well as higher larval survival, higher

larval dry weight, and higher oviposition correlated to high phloem moisture contents. Finally, Wainhouse *et al.* (1998) observed that wounding had positive effects on adult gallery size and establishment, and that nitrogen and starch were more abundant after wounding.

A last intriguing aspect is the stable mean number of attacks per tree illustrated by Fig. 4, even though the total population in the stand grew exponentially (Fig. 2). As a live host is vital for the long-lived *D. micans*, whose life cycle often exceeds 2 years (Grégoire, 1988), limited pressure on the host is required. Leaving the natal host tree might also provide an escape from natural enemies. Even though changing trees might not necessarily provide long-term avoidance of specific predators with a high searching capacity, such as *Rhizophagus grandis* [in Belgium, >90% of the broods are eventually discovered by *R. grandis* (Grégoire, 1988)], moving to new trees could delay discovery by *R. grandis*, thus allowing a higher proportion of the bark-beetle broods to survive. The mechanisms that cause these stable attack levels per tree are totally unknown. *Dendroctonus micans* might produce an epideictic pheromone responsible for keeping attack level below a threshold lethal to the tree. Another possibility could be connected to the hypothesis of induced tree susceptibility that was developed earlier: if spots favourable for new attacks are located mostly above or below earlier attacks, there is limited room for more than a few new colonisers.

Further experiments and analyses could be developed to confirm and expand the hypotheses developed here. First, the total absence of spatial dependence of attack counts per tree in this study calls for spatial analyses at larger scales. They might provide information on the insect's dispersal ability and on the unknown effects of environmental features on dispersal and establishment. Second, individual tree characteristics such as growth rates and phloem quality could be analysed to discuss further the tree susceptibility model.

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