



Multiscale spatial variation of the bark beetle *Ips sexdentatus* damage in a pine plantation forest (Landes de Gascogne, Southwestern France)

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ABSTRACT

Bark beetles are notorious pests of natural and planted forests causing extensive damage. These insects depend on dead or weakened trees but can switch to healthy trees during an outbreak as mass-attacks allow the beetle to overwhelm tree defences. Climatic events like windstorms are known to favour bark beetle outbreaks because they create a large number of breeding sites, i.e., weakened trees and for this reason, windthrown timber is generally preventively harvested and removed. In December 1999, the southwest of France was struck by a devastating windstorm that felled more than 27 million m³ of timber. This event offered the opportunity to study large-scale spatial pattern of trees attacked by the bark beetle *Ips sexdentatus* and its relationship with the spatial location of pine logs that were temporally stored in piles along stand edges during the post-storm process of fallen tree removal. The study was undertaken in a pure maritime pine forest of 1300 ha in 2001 and 2002. We developed a landscape approach based on a GIS and a complete inventory of attacked trees. During this study more than 70% of the investigated stands had at least one tree attacked by *I. sexdentatus*. Spatial aggregation prevailed in stands with $n \geq 15$ attacked trees. Patches of attacked trees were identified using a kernel estimation procedure coupled with randomization tests. Attacked trees formed patches of 500–700 m² on average which displayed a clumped spatial distribution. Log piles stemming from the sanitation removals were mainly distributed along the large access roads and showed an aggregated spatial pattern as well. The spatial relationship between patches of attacked trees and log pile storage areas was analyzed by means of the Ripley's statistic that revealed a strong association at the scale of the studied forest. Our results indicated that bark beetle attacks were facilitated in the vicinity of areas where pine logs were stored. The spatial extent of this relationship was >1000 m. Similar results were obtained in 2001 and 2002 despite differences in the number and spatial distribution of attacked trees. The presence of a strong "facilitation effect" suggests that log piles should be removed quickly in order to prevent outbreaks of bark beetles.

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1. Introduction

Bark beetles are notorious pests of natural and planted forests causing extensive damage. Most bark beetles depend on dead or weakened trees but aggressive species switch to healthy trees during epidemic outbreaks. There is a wealth of literature showing that successful bark beetle attacks of living trees occur when a pioneer insect manages to recruit a sufficient number of individuals through the release of aggregation pheromone (Lieutier et al., 2004). During such mass-attacks, insects can overwhelm tree defenses and generally kill it (Berryman et al., 1989). Among others factors, windthrown timber is considered to

trigger or favour bark beetles outbreaks because they offer large amounts of available resource on which insects can build up their populations (Reynolds and Holsten, 1994; Eriksson et al., 2005; Gilbert et al., 2005). As a consequence, windthrown timber is generally harvested in order to preventively remove breeding substrate for bark beetles (Wermelinger, 2004). After windstorms, large amounts of wind-felled logs are gathered and progressively removed. An increase of the number of attacked trees can be expected nearby important log storage areas if storage period coincides with adult flight. Different ecological factors affect bark beetle population dynamics and spatial distribution at various spatial and temporal scales. Individual trees display different levels of resistance due to genetic characteristics (Lieutier et al., 2003; Rosner and Hannrup, 2004) or particular physiological conditions following environmental disturbances like fire (Fernandez, 2006) or drought (Rouault et al., 2006). At the stand scale, the position of individual trees with respect to stand edge and/or clearcuts is

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important because the turning moment of the wind is more powerful and microclimate changes more suddenly near forest edges (Peltonen, 1999). At the landscape scale, bark beetle distribution is affected by various factors like the spatial arrangement of stands, the distribution of forest roads or the stand age classes. Log piles are preferentially stored near access roads. Their distribution therefore reflects management options and landscape structure and may dramatically affect the spatial pattern of bark beetles populations. Although the mechanisms by which bark beetles colonize individual living trees are well understood there is still a limited amount of spatially explicit information on the pattern of attacks and most notably studies at the landscape scale are lacking (but see Coulson et al., 1999; Gilbert et al., 2005; Gilbert and Grégoire, 2003).

In this paper, we tackle the question of the relationship between log piles of wind-felled pines and the attacks of the bark beetle *Ips sexdentatus* (Boern) (Coleoptera, Scolytidae) in a spatially explicit framework. We reanalyzed a data set previously published by Samalens et al. (2007). The data were collected in a pure maritime pine plantation forest (*Pinus pinaster*, Aiton 1789) following the devastating windstorm that struck southwestern France in December 1999 and felled more than 27 million m³ of timber.

2. Material and methods

2.1. Study site

The data were collected in the plantation forest of Lagnereau located in the Landes de Gascogne, Southwestern France (44°30'N,

1°14'W). This forest is a 1300 ha mosaic of pure maritime pine stands (*P. pinaster*). The study spanned 2 years (2001 and 2002) (Fig. 1) following an important windstorm that occurred in 1999. The spatial location of each tree attacked by *I. sexdentatus* and the pine log piles were recorded in both years (see below). The log piles were several metres high for a length of ca. 100 m or more in some cases.

2.2. Spatial database

A complete inventory of attacked trees was undertaken in autumn 2001 and 2002 by means of colour infrared photographs of high spatial resolution (Samalens et al., 2007). An exhaustive ground sampling was conducted in 2001 in order to establish the cause of decay or mortality of all damaged trees in the central part of the forest (19 stands) and to calibrate the photo interpretation phase. Information about every stand edge in the forest, the position of log piles and the exact location of all trees attacked by *I. sexdentatus* were stored in a geodatabase (Samalens et al., 2007). The database was complemented using additional information indicating the position of the log piles that were removed before the aerial survey was carried out.

2.3. Statistical analyses

The Lagnereau forest comprised stands of different ages that corresponded to different tree densities. This point is important because the methods used to analyze spatial point patterns have been developed for homogeneous point patterns (Pélissier and Goreaud, 2001). In this study, the latter assumption is not met at

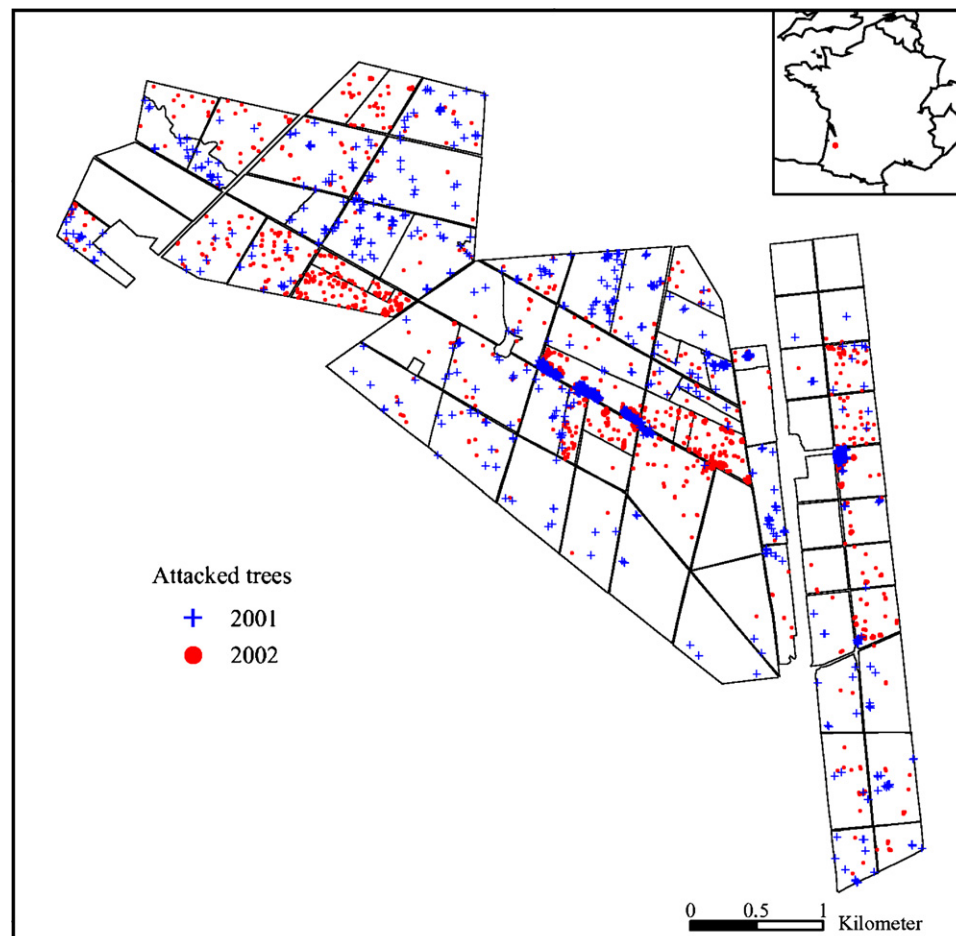


Fig. 1. Map of trees attacked by the bark beetle *I. sexdentatus* in 2001 and 2002 in a pine plantation forest (Landes de Gascogne, Southwestern France).

the landscape scale and we therefore adopted different strategies according to the spatial scale considered (stand or landscape). We used the Ripley's function (Ripley, 1981) to examine the spatial pattern of attacked trees at the stand scale. Attacked trees formed patches and we described these structures by means of kernel estimates. Once the patches were mapped we analyzed their spatial pattern and its relationship with the distribution of log piles using a modified Ripley's function especially dedicated to processing objects (patches, log piles) instead of points (trees) (Wiegand et al., 2006).

2.4. Stand scale analyses

2.4.1. Point pattern analysis

The spatial distribution of the trees attacked by *I. sexdentatus* was analyzed by means of the Ripley's statistic (Ripley, 1981; Fortin and Dale, 2005). The Ripley's K is based on the idea that if λ is the density of points (attacked trees) per unit area, the expected number of points in a circle radius t centred on a randomly chosen point is $\lambda K(t)$ where $K(t)$ is a function of t that depends on the point pattern. $K(t)$ is estimated as:

$$\hat{K}(t) = \frac{A \sum_{i=1}^n \sum_{\substack{j=1 \\ j \neq i}}^n \omega_{ij} I_t(i, j)}{n^2}$$

where A is the studied area, $I_t(i, j)$ is an indicator function taking the value of 1 if the distance separating points i and j is less or equal to t and 0 otherwise, n is the total number of points and ω_{ij} is a weight that corrects for edge effects. We used the border correction proposed by Ripley (1988). Bias on $\hat{K}(t)$ may become appreciable for point patterns consisting of fewer than 15 points (Baddeley and Turner, 2005) and therefore Ripley's K analysis was used for stands featuring at least 15 attacked trees. We used Monte Carlo technique to test for departure from complete spatial randomness (CSR) (Diggle, 2003). A large number (1000) realizations of CSR for densities $= \lambda$ was generated and $\hat{K}(t)$ estimated. For every distance value t , a local confidence interval was built using the first percentile method (Manly, 1997), i.e., the interval corresponded to the quantiles for $p_1 = 0.025$ and $p_2 = 0.975$ ($\alpha = 0.05$). Observed $\hat{K}(t)$ larger than the upper limit of the envelope indicated significant aggregation while values lower than the lower bound denoted regular patterns. In this paper we used a transformed value of Ripley's K function namely the Ripley's L statistic, $L(t) = \sqrt{\hat{K}(t)/\pi}$. The transformation is useful because it stabilizes the variance and linearizes the plot of $L(t)$ against t (Ripley, 1981). We used the statistical software R (R Development Core Team, 2008) and the associated package `spatstat` (Baddeley and Turner, 2005) to perform these computations.

2.4.2. Patch of attacked trees

Our approach to patch identification and description consisted of a two-step process. First, a kernel density estimate (Cressie, 1993) was used to assess the density of the point pattern (here, points are attacked trees) at the nodes of a systematic grid of $2 \text{ m} \times 2 \text{ m}$. Second, we used a Monte Carlo approach in order to identify grid nodes associated with densities significantly higher than expected under the null hypothesis of complete spatial randomness of attacked trees.

The kernel density interpolation provides density estimates at different locations, e.g., the nodes of a systematic grid. A symmetrical probability function, the kernel, is placed over each point location and the underlying density distribution is estimated by summing the individual kernel functions (Cressie, 1993). We used the value of the resulting function at each node of the systematic grid to build density maps. We employed a normal kernel density estimator (Kelsall and Diggle, 1995) with a

bandwidth (i.e., the width of the kernel function) following Silverman's "rule of thumb" (Silverman, 1986, p. 48) as slightly modified by Scott (1992). Density estimates were corrected for edge effect bias by dividing them by the convolution of the normal kernel function with the window of observation as proposed in the R package `spatstat` (Baddeley and Turner, 2005).

The statistical significance of the kernel estimates derived from the observed pattern of attacked trees was assessed by comparison with estimates from randomly distributed trees. The null hypothesis is that of a complete spatial randomness (CSR) of attacked trees. The conditions of such hypothesis were simulated using a Poisson point process (Diggle, 2003). A number of 1000 simulations were done for each forest stand and used to build the frequency distribution of the attacked tree density under the null hypothesis of CSR for each grid node location. If the observed kernel estimate was larger than the distribution quantile for $p = 1 - \alpha$, it was considered statistically significant at the type I error α . Grid points associated with significant and non-significant values were used to construct a categorical raster map showing areas associated with high densities of attacked trees.

2.5. Landscape scale analyses

Stand level information was aggregated to form a landscape raster map comprising 3 types of pixels: matrix pixels, patches of attacked trees and log piles. Patches were smoothed so that each pixel associated with a significant value was not separated from an attacked tree by more than 5 m. This map was investigated using the software `Fragstats` (McGarigal et al., 2002) in order to compute the number of patches of attacked trees, their average surface and the percentage of the landscape they covered.

The former raster map was analyzed with the modified Ripley's index proposed by Wiegand et al. (2006) to (i) assess the spatial distribution of patches and log piles separately and (ii) to test for spatial co-variation between them. This new approach extends Ripley's index to deal with objects of finite size and irregular shape instead of points. In our case, patches or log piles were approximated by using the underlying grid of the raster map and occupied several adjacent grid cells depending on their size and shape. We used the bivariate Ripley's L (Wiegand et al., 2006) to assess the way patches of attacked trees and log piles co-varied in space whereas the univariate modified Ripley's L allowed us to examine the variables separately.

The analysis of the relationships between patches of attacked trees and log piles focused on the facilitation hypothesis (Wiegand et al., 2006). Facilitation exists if patches of attacked trees occur more frequently in the neighbourhood of log piles than expected under a random distribution of patches of trees. In our case, the appropriate null model is the "antecedent condition" model in which the log piles were fixed whereas the patches of attacked trees were randomly distributed over the area not occupied by log piles (Wiegand and Moloney, 2004). As before, significant departure from the null models was assessed using Monte Carlo randomizations. We used the software `Programita` (Wiegand et al., 2006) and performed 2000 randomizations for each test.

3. Results

3.1. Spatial distribution of attacked trees at the stand scale

A total of 2392 and 3138 attacked trees were identified and mapped in 2001 and 2002, respectively. The corresponding densities ranged from 2 to 3.1 tree ha^{-1} . A large number of stands (71 and 73%) exhibited attacked trees (Table 1) with counts ranging from 0 to 927 and 0 to 738 in 2001 and 2002 respectively. Only the stands showing $n \geq 15$ attacked trees (28 and 31% in 2001 and 2002) could

Table 1
Descriptive statistics for the occurrence of trees attacked (AT) by the bark beetle *I. sexdentatus* and the patches they form within a pine plantation forest (Landes de Gascogne, Southwestern France) in 2 consecutive years. The number of investigated stands was 82 and 81 in 2001 and 2002 respectively.

	2001	2002
Total attacked trees (AT) (range per stand between brackets)	2392 (0–927)	3138 (0–738)
Mean AT ha ⁻¹ (standard error per stand between brackets)	2.0 (0.86)	3.1 (0.9)
Stands with 0 AT	24 (29.3%)	22 (27.2%)
Stands with AT	58 (70.7%)	59 (72.8%)
Stands with $n \geq 15$ AT	23 (28.0%)	25 (30.9%)
Stands with $1 < n < 15$ AT	35 (42.7%)	34 (42.0%)
Stands with aggregated AT	23	24
Stands with aggregated AT and $n \geq 15$ AT	100.0%	96.0%
Stands with random distribution of AT	0 (0%)	1 (1.2%)
Number of patches of attacked trees (AT)	148	38
Mean patch area (m ²) (standard deviation between brackets)	743.2 (113)	515.8 (95.8)
Maximum patch area (m ²)	11900	3500
Percentage of landscape occupied by patches of AT	0.80 (%)	0.15 (%)

be investigated using the Ripley's approach and most showed an aggregated spatial distribution of attacked trees (Table 1).

Fig. 2 A depicts the case of highly aggregated attacks in 2001 and 2002. In 2001 attacked trees formed 3 clear patches representing a total of 927 trees whereas 426 trees were recorded in 2002. The attacked trees were logged and removed from the stand between 2001 and 2002. In 2002, the number of attacked trees was lower but they were strongly aggregated and formed patches mostly located at the edges of the stands in places where the 2001 attacks were concentrated. Some stands showed aggregated attacked trees in 1 year and not in the other. Fig. 2 B shows a large patch of attacked trees at the centre of the stand ($n = 59$, 2001) while no aggregation

occurred in 2002. This is the only record of a large patch occurring at the centre of a stand, aggregation being generally localized near the edges. Fig. 2 C shows randomness in 2001 and aggregation in 2002 ($n = 96$) with 3 very clear patches. Fig. 2 D depicts the only stand with a random spatial pattern of attacked trees (2002, $n = 26$).

3.2. Spatial distribution of patches of attacked trees and their relationships with the location of log piles across landscape

Kernel density estimations and the associated randomization test led to raster maps that were analyzed using landscape metrics (Table 1). The number of patches of attacked trees and the

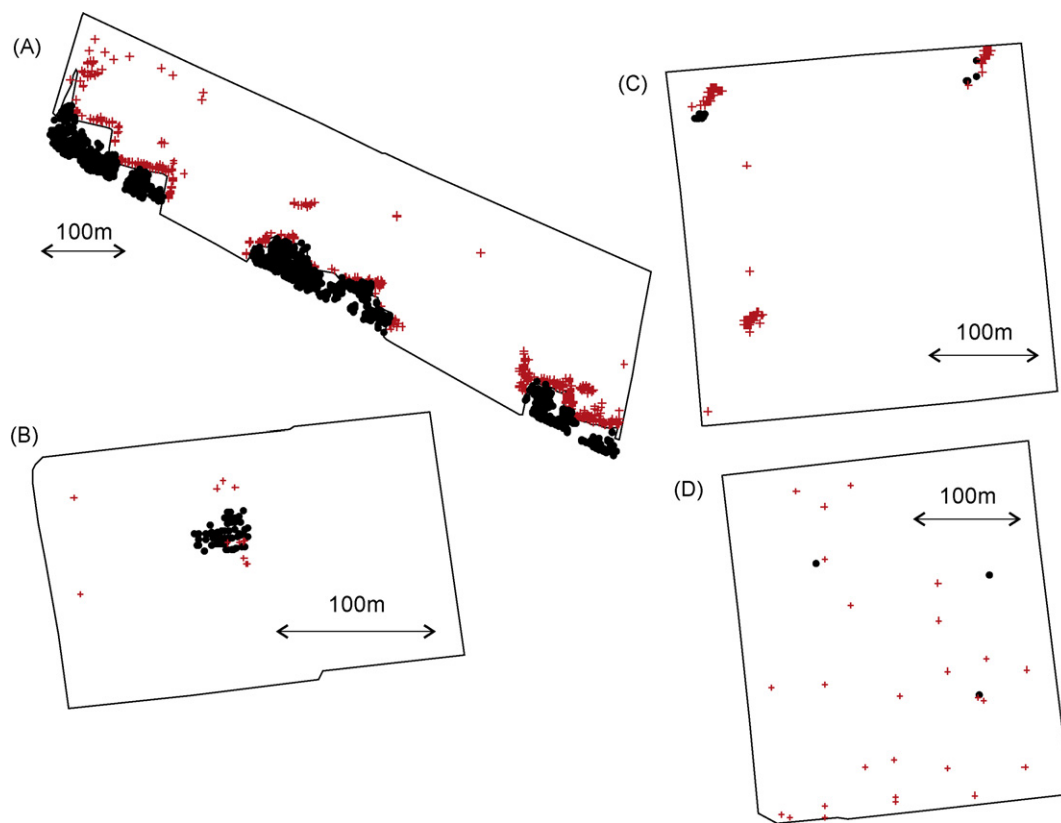


Fig. 2. Examples of stand scale spatial distribution of trees attacked by the bark beetle *I. sexdentatus* in pine plantation forest (Landes de Gascogne, Southwestern France). Dots: 2001, crosses: 2002. (A) Aggregation of attacked trees in 2001 and 2002. (B) Large patch in the centre of the stand in 2001 and spatial randomness in 2002. (C) No significant aggregation in 2001 while 3 patches were observed in 2002. (D) The only case of random spatial distribution for stands with $n \geq 15$ occurred in 2002. In 2001 the number of attacked trees was too low to allow statistical analysis of this stand.

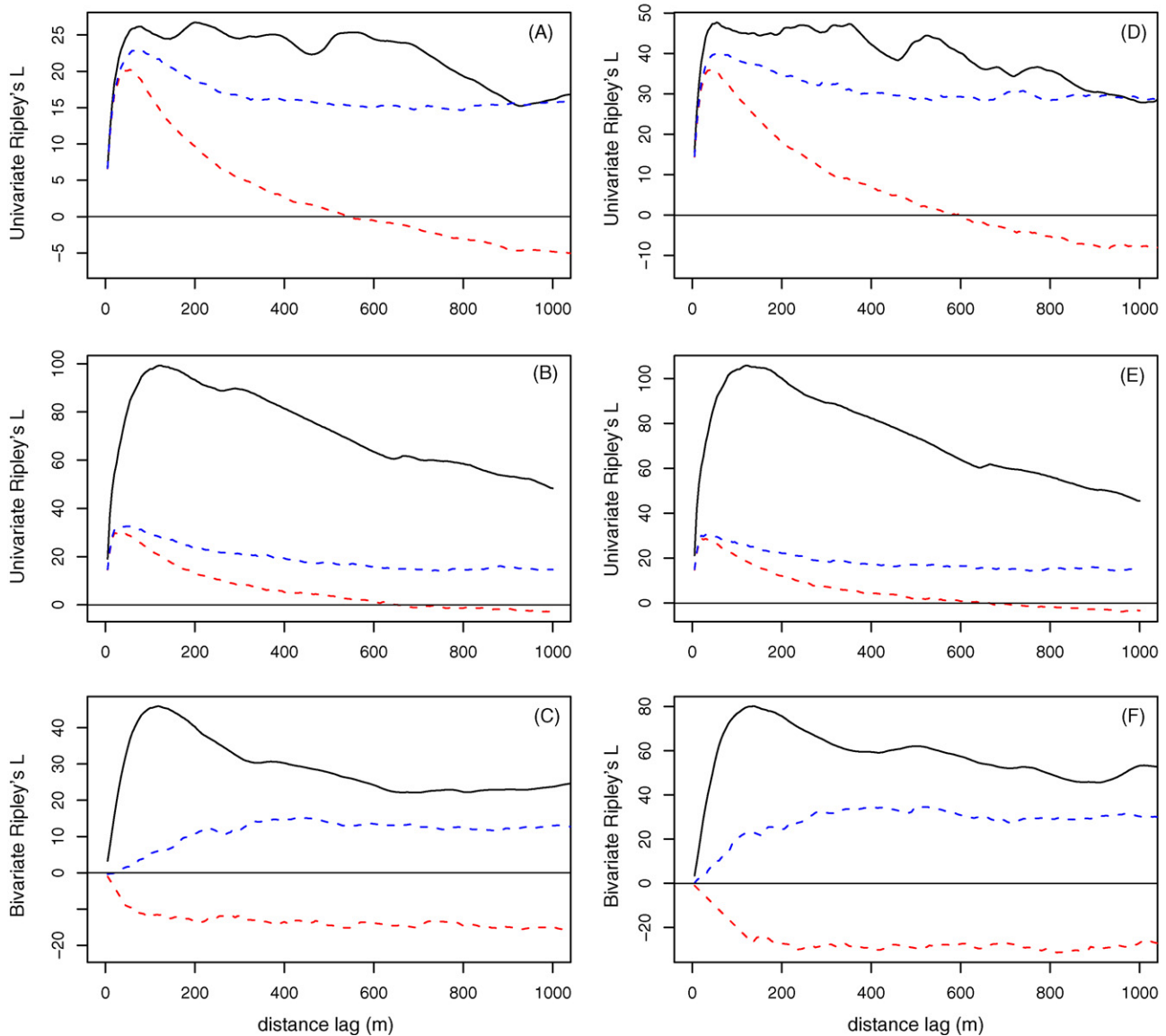


Fig. 3. Modified Ripley's uni- and bivariate L functions and associated statistical envelopes ($\alpha = 0.05$) for the patches of trees attacked by the bark beetle *I. sexdentatus* and the log piles in 2001 and 2002. (A) Univariate modified L function for patches of attacked trees in 2001. (B) Univariate modified L function for log piles in 2001. (C) Bivariate modified L function for patches of attacked trees and log piles in 2001. (D) Univariate modified L function for patches of attacked trees in 2002. (E) Univariate modified L function for log piles in 2002. (F) Bivariate modified L function for patches of attacked trees and log piles in 2002.

percentage of landscape they covered decreased between 2001 and 2002 (Table 1). Similarly, the number of log piles recorded in 2002 was lower than in 2001 (83 and 103 log piles respectively).

The modified Ripley's L analysis (Wiegand et al., 2006) showed that the patches were strongly aggregated in 2001 and 2002 (Fig. 3 A and B) since the observed univariate L function was above the upper 97.5% limit for distance < 900 m. The patch distribution tended towards randomness for distance ≈ 900 m both in 2001 and 2002. Similarly, the log pile distribution was aggregated in both years (Fig. 3 B and E). The modified bivariate Ripley's L function revealed the presence of a strong positive association between the log piles and the patches of attacked trees in 2001 and 2002. This relationship tended to weaken for distances of ca. 800–900 m but remained highly significant (Fig. 3 C and D).

4. Discussion

The present study showed the existence of a positive relationship between the bark beetle *I. sexdentatus* attacks of healthy trees

and the presence of cut log piles. More specifically, we showed that bark beetles attacks were facilitated in the vicinity of areas where pine logs were stored. The spatial extent of this relationship was ≥ 1000 m. These results are consistent with the conclusions drawn from various studies that showed successful attacks to be located close to fallen or broken trees or piles of cut logs on which bark beetles have previously built up their population (Fettig et al., 2007; Peltonen et al., 1998; Wichmann and Ravn, 2001; Grodzki et al., 2006).

4.1. Nested spatial scales

At the stand scale, the spatial distribution of attacked trees was generally aggregated when the number of attacked trees was ≥ 15 . This is in accordance with the well-known aggregative behaviour of most bark beetles (Berryman et al., 1989). Interestingly, aggregation corresponded to diverse patterns of patches with very different sizes and shapes. When larger spatial scales were considered it appeared that hot spots of attacks were still clustered

and formed what we refer to as “patches of patches”. The clusters of patches may be partly due to an aggregated distribution of the log piles themselves which in turn reflects the uneven spatial distribution of windstorm damage and/or the distribution of forest roads along which the log piles were stored. This suggests that the pattern of forest damage by bark beetles may result from interactions between forest management, topography, prevailing winds and existing forest path networks.

4.2. Long-range distribution and dispersal of *I. sexdentatus*

The spatial association of log piles and attack densities was observed along a continuum of spatial scales and it was still significant at 1000 m. Therefore the impact of log piles storage on bark beetle infestations had a somewhat large spatial extent. Bark beetles are known to have very good dispersion abilities and it is an essential element of their biology (Sauvard, 2004). The breeding substrate (phloem or inner bark) is destroyed at each generation and emerging adults have to migrate. Because they are unable to successfully colonize healthy trees in the endemic conditions they have developed high capacities to disperse and find suitable hosts. It has been reported that they can fly tens of kilometres (Jactel, 1991; Wermelinger, 2004). If log piles act as a source of emerging beetles, high dispersal leads to large-scale positive effects of log piles storage sites upon attacks which is what we found using the modified Ripley's *L* function. The spatial extent of the correlation between log piles and patches of attacks has also some consequences in terms of experiment design. Because this relationship corresponds to some degree of autocorrelation (i.e., spatial dependence) it should ideally be accounted for when designing experimental systems as well as during the process of data treatment (Legendre et al., 2002).

4.3. Statistical definition and analysis of bark beetle hot spots of attacks

The results of the present survey were in accordance with the well-known fact that fallen or cut trees are good breeding sites and can trigger bark beetle mass-attacks (Peltonen, 1999; Reynolds and Holsten, 1994; Eriksson et al., 2005). The novelty is that we found different levels of spatial structures corresponding to different scales. Studying such complex spatial patterns required an important amount of spatial information organized in a GIS. At the stand scale the Ripley's *L* function appeared to be well suited to study the distribution of attacked trees (see e.g., Chen and Bradshaw, 1999) but other complementary analyses were necessary at larger spatial scales. The kernel approach proved to be an interesting tool to identify hot spots of attacked trees and to delimit these clusters although alternative approaches may work as well (Pélissier and Goreaud, 2001). The modified Ripley's *L* function (Wiegand et al., 2006) is powerful and its ability to account for the object shape allowed us to precisely analyze the relationships between location of log piles and hot spots of bark beetle attacks. Using this combined approach provided a multi-scale view of *I. sexdentatus* spatial distribution and illustrated the relationships between cut log piles distribution and foci of forest damage. More generally, such data treatments could also be very useful in forest pathology and epidemiology because the description of spatial clusters is the first step towards identification of the ecological factors from which they originate. The existence of a marked log pile effect in 2001 and 2002 has interesting implications in terms of forest pest sampling and monitoring. In a previous paper (Samalens et al., 2007) we showed how the presence of log piles could be of great help in designing road sampling programmes to assess bark beetles infestations. Because of their strong co-variation with hot spots of attacks, log

piles can be taken as a stratification factor and used to improve sampling protocol and monitoring programmes (Samalens et al., 2007).

4.4. Temporal variability

Our study spanned 2 consecutive years and although the overall number of attacked trees, their spatial pattern, the number of patches, their size and their surface varied dramatically, we found a comparable effect of log piles. In 2002, the total number of attacked trees increased while the surface area of the patches decreased. This indicated a change in the spatial distribution of the attacks that tended to be more clumped. We lack comparable studies and therefore it is not possible to know if such changes in the spatial arrangements of attacked trees are usual. There is an obvious gap in our knowledge of the spatial dynamics of bark beetle outbreaks and most notably we did not analyze patterns of aggregation over the course of an outbreak. *I. sexdentatus* is a plurivoltine species that can have up to 3 generations during favourable years. The trees that were damaged in December 1999 by the windstorm were progressively removed and constituted good quality material for the first and probably the second generation of insects that developed in Spring/Summer of 2000. This resource was likely to be exhausted for the third generation (if any) but there were still numerous wind-felled pines with varying degree of root connection. We hypothesize that these trees have hosted the third generation of insects in 2000. Sanitation removals conducted in late 2000 and throughout the first part of 2001 led to the storage of logs that hosted numerous insects that emerged in Spring 2001 and mass-attacked healthy trees. Recent studies showed that keeping a small number of wind-felled trees did not lead to noticeable increases of tree mortality by *I. typographus* (Eriksson et al., 2007, 2008; Hedgren et al., 2003). Such management options must be examined carefully because they promote the retention of more dead wood in managed forests. Dead wood is an important substrate and habitat for a large number of species that should be protected (Bouget and Duelli, 2004). Our survey focused on a population during its epidemic stage and our results indicate a strong effect of cut logs. However, our conclusions do not apply to populations during the endemic phase and therefore are not in contradiction with the conclusions of Eriksson et al. (2007, 2008) or Hedgren et al. (2003). Moreover our results were obtained in a monospecific plantation forest and additional studies involving different forest types, tree and insect species would be needed to generalize the scope of our conclusions.

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