

Research article

Post-storm surveys reveal large-scale spatial patterns and influences of site factors, forest structure and diversity in endemic bark-beetle populations

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Abstract

The storm that struck France on december 26th and 28th 1999 felled 140 million m³ of timber and had a high economic, social and landscape impact. This event offered the opportunity to study large-scale patterns in populations of forest insect pests that would benefit from the abundant breeding material. A large-scale survey was carried out in France in 2000 to sample the most frequently observed species developing on spruce (*Ips typographus*, *Pityogene schalcographus*) and pine (*Tomicus piniperda*, *Ips sexdentatus*) in 898 locations distributed throughout wind-damaged areas. The local abundance of each species scored on a 0 to 5 scale was analysed using geostatistical estimators to explore the extent and intensity of spatial autocorrelation, and was related to site, stand, and neighbourhood landscape metrics of the forest cover (in particular the interconnection with broadleaf forest patches) found within dispersal distance. All species but *I. sexdentatus*, which was much less abundant, displayed large-scale spatial dependence and regional variations in abundance. Lower infestation levels per tree (windfalls and standing trees) were observed in stands with a high proportion of wind-damaged trees, which was interpreted as the result of beetles distributing themselves among the available breeding material. More infestations were observed in wind-broken trees as compared to wind-felled trees. More importantly, populations showed significant relationships with the structure of coniferous stands (in particular with the number of coniferous patches). *T. piniperda* population levels were negatively correlated to the amount of coniferous edge shared with broadleaf forest patches, possibly because of the disruptive effect of non-host volatiles on host-finding processes at the landscape-scale. The differences observed between species regarding patterns and relationships to site, stand, and forest cover characteristics are discussed in relation to the ecological characteristics of each species.

Introduction

Bark-beetles are serious pest of planted and natural forests causing important damages when population outbreaks occur (e.g., 500,000 m³ of spruce were killed by *Ips typographus* and *Pityogene schalcographus* between 1992 and 1994 following the storms that struck northeastern France in 1990; Nageleisen 2000). Primary species are able to attack and kill

apparently healthy trees, and therefore constitute the most immediate threat. However, secondary species (species usually able to infest only host trees of reduced vigour) are capable of developing primary attitudes and cause significant damage when their populations reach epidemic levels (Coulson 1979). Bark-beetle population outbreaks are generally triggered, or facilitated by, climatic events such as storms [e.g., lightning strikes in *D. frontalis* (Coulson et al.

1999), windfelled trees in *I. typographus* (Göthlin, Schroeder and Lindelow 2000)], droughts (e.g., *D. micans*; Grégoire 1988) or a combination of these factors (*D. pseudotsugae*; Powers et al. 1999). On december 26th and 28th 1999, a devastating storm struck France and felled 140 million m³ of timber (Landmann et al. 2000), with catastrophic economic, social and landscape impact. Apart from *Dendroctonus micans* (Kug.), an invasive pest of spruce still expanding its range in France and which attacks only apparently healthy trees (Grégoire 1988) and is not influenced by the effects of storms, all bark beetles attacking production woodlands in France are endemic. These species were therefore expected to breed and expand in every area where the storms had provided new resources, i.e., the whole of France except the southeast and the Pyrenean mountains. This situation provided a unique opportunity for a large-scale study of the pre-storm populations as revealed in the vast amount of breeding material suddenly made available. The French Forest Health Department (DSF, France) hence undertook survey in 2000 and 2001 to assess population levels at the national scale.

Large-scale spatial patterns in bark-beetle populations were studied in several North-American species such as the bark beetles *Dendroctonus frontalis* (Gumpertz, Chi-Tsung and Pye 2000; Coulson et al. 1999), *Dendroctonus spseudotsugae* (Powers et al. 1999; Negron 1998) or *Dendroctonus adjunctus* (Negron, Wilson and Anhold 2000). In contrast, very few data are available on large-scale distribution patterns of European bark-beetle species, and the literature largely addresses a local scale and spatial patterns at the scale of the stand (*I. typographus*: Peltonen 1999; Göthlin, Schroeder and Lindelow 2000; Franklin 2001; *D. micans*: Gilbert and Grégoire 2003), or the landscape (*I. typographus*: Franklin 2001; *D. micans*: Gilbert et al. 2003). Using DSF survey data of the first sampling period, i.e., reflecting pre-storm endemic population levels, large-scale distribution patterns in four of the most important European bark-beetles of spruce (*I. typographus*, *P. chalcographus*) and pine (*Tomicus piniperda*, *Ips sexdentatus*) were submitted here to two types of analyses.

On the one hand, the intensity and extent of spatial autocorrelation (SA) in beetle populations at the national scale was explored. SA, or spatial dependence, is the tendency of points close to each other to have more similar values than points farther apart. Quantifying SA is important for three reasons. Firstly, it

may help inferring the balance between local and regional processes affecting beetle population dynamics. Populations with strong SA over long-distance are likely to be influenced by factors occurring at a large spatial scale (e.g., climate, regional landscape structure), whereas populations with no SA are likely to have most of their variability related to local effects already identified for European bark-beetles [e.g., clearcut and thinnings (Peltonen 1999; Thiel 1999), site and stand conditions affecting host suitability (Gilbert and Grégoire 2003; Reeves, Ayres and Lorio 1995), management schemes (Franklin 2001)]. Secondly, quantifying SA would allow adjusting future sampling designs according to the intensity and range of autocorrelation (Fortin, Drapeau and Legendre 1989). Thirdly, SA would need to be taken into account in the statistical analysis of population levels vs. environmental predictors (Legendre et al. 2002; Keitt et al. 2002).

On the second hand, we tried to identify quantitative relationships between population levels and covariates at the local (i.e., within-patch characteristics) or landscape scale (involving several forest patches). If these relationships reflect genuine ecological relationships, they might improve our understanding of bark-beetle ecology, and be used in the future for risk assessment to identify high priority intervention areas (Berryman 1986). The effect of three types of factors were tested here: site factors describing the physical environment of the sampling locations, stand factors such as tree size or the level of local wind damage, and landscape factors describing stand structure in the nearby neighbourhood. Several authors have already analysed the local effects of site and stand factors on population levels of the bark-beetle species studied here (e.g., *I. typographus* and *P. chalcographus*: Göthlin, Schroeder and Lindelow 2000; Franklin 2001; Dutilleul, Nef and Frigon 2000; *T. piniperda* and *I. sexdentatus*: Amezaga 1997; Schlyter and Löfqvist 1990), and thus the present approach might confirm the influence of these local effects observed from a very large spatial scale. The impact of the factors related to landscape structure in the neighbouring stands has already been reported in several North-American forest insect pests (e.g., Roland 1993; Coulson et al. 1999), and, at the local scale in several European bark beetles. For example, forest edges have been showed to be favoured by some species (*I. typographus*, *P. chalcographus*, *T. piniperda*: Peltonen 1999; Göthlin, Schroeder and Lindelow 2000; Peltonen, Heliövaara and Väisänen

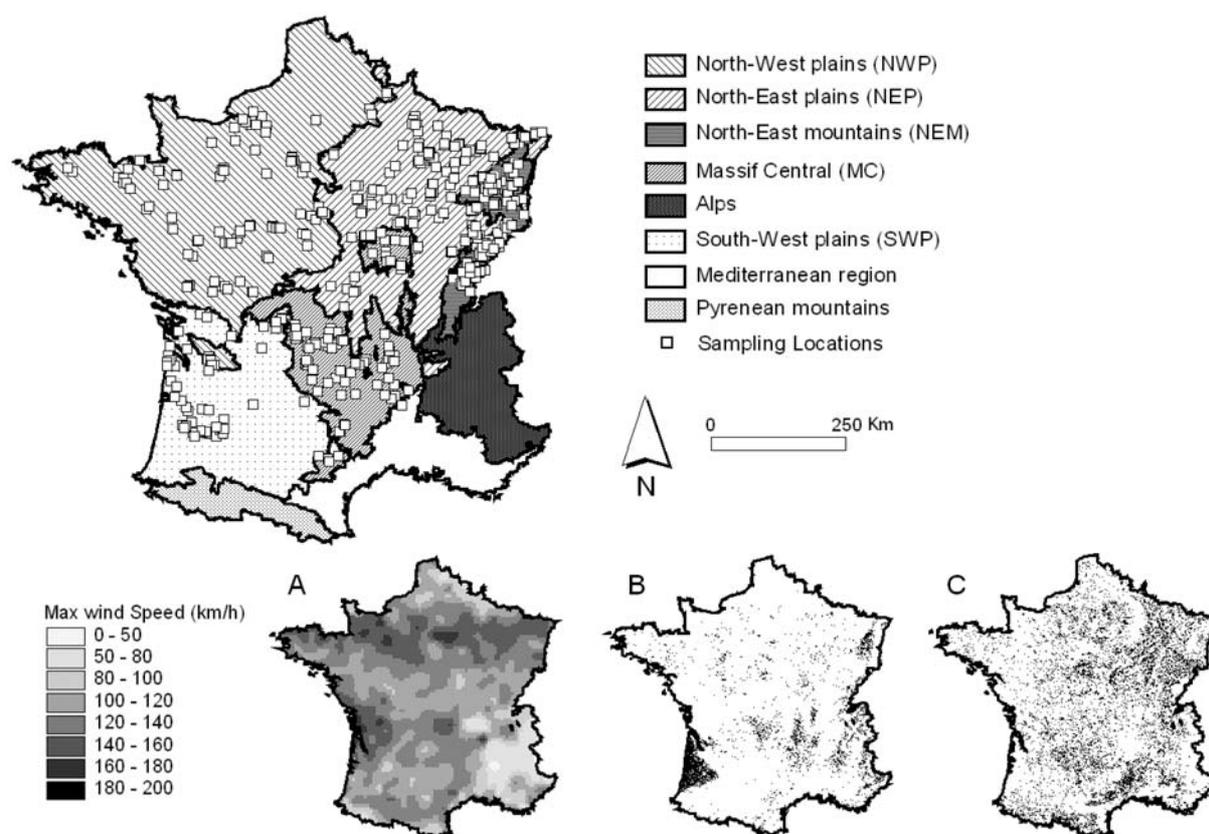


Figure 1. The monitoring network and ecological regions (top), the maximum wind speed recorded over the 26th and 28th December 1999 (A) (Landmann et al. 2000), the distribution of coniferous (B) and broadleaf (C) forests as classified in the CORINE LandCover database (CEC 1994).

1997) and avoided by other bark beetles (*Xylechinus pilosus*, *Cryphalus saltuarius*: Peltonen and Heliovaara 1998). The species studied here are reported to favour forest edges and fragmented landscapes with convoluted forest patches would thus be expected to present higher infestation levels. Another important factor potentially affecting bark-beetle populations at the landscape scale is the repellent effect of non-host volatiles (NHV) that has been demonstrated in the coniferous bark-beetle species studied here (*I. typographus*: Zangh and Schlyter 2003; *P. chalcographus*: Byers et al. 1998; *T. piniperda*: Poland and Haack 2000 and *I. sexdentatus*: Jactel et al. 2003). Although the use of such repellents has been tested successfully for the protection of individual trees or piles of logs, only one work to our knowledge (concerning the pine stem borer *Diorctria sylvestrella*; Jactel et al. 2002) presented experimental evidence of NHV disruption of a coniferous pest infestation at the landscape scale. Relating population levels as measured in the

nationwide survey to landscape metrics describing the structure of the forest cover would allow testing some of these hypotheses, or at least, establishing if these relationships translate into patterns measurable at large scale.

Materials and methods

Data

250 forest officers were organised in a network established in 2000 by the French Department of Forest Protection (Landmann et al. 2000) to monitor bark-beetle populations in forest areas most damaged by the storms (Figure 1a). The survey included sites composed of pine (287), spruce (220), oak (139), beech (83), douglas fir (82), fir (65), and a few other tree species more scarcely represented in the survey (22). Five wind-felled or wind-broken trees of the

same species and distant from each other by more than 20 m (such as to exclude adjacent trees) were selected before insect emergences, and were surveyed in each site. The presence/absence of the following insects was recorded on six sections on the trunk: *Ips typographus*, *Pityogenes chalcographus*, *Ips sexdentatus*, *Tomicus piniperda*, *Ips acuminatus*, *Orthomicuserosus*, *Pissodes notatus*, *Pityokteines* sp., *Pissodes piceae*, *Cryphalus picea*, ‘unspecified scolytids’ and ‘unspecified xylophages’. Sites were visited in May – June 2000 for the first visit and in August – early October 2000 for the second visit. An additional visit was carried out in March 2000 in sites where *T. piniperda* could potentially have been observed (*Pinus* sp.). Population were estimated by the number of trees infested per site (0 to 5) and the total number of tree sections infested per site (0 to 30). A general score was estimated reflecting the number of trees infested per site regardless of the insect species or category involved (0 to 5).

Several site factors were recorded at the time of survey: site geographical location, main tree species, site aspect, local topography, slope, elevation, average tree age, average tree height, average tree diameter and estimated proportion of undamaged trees in the stand. The proportion of wind-felled trees (all sampled trees were either wind-felled or wind-broken) among the 5 sampled trees was also estimated in each site.

In addition to these field observations, data on the forest cover in the vicinity of the sites were used to test its possible impact on beetle population levels. Forest cover data were extracted from the Corine Land Cover raster database published by the European Commission classifying the European land cover at a resolution of 6.25 ha (CEC 1994). The classes ‘Coniferous forest’, ‘Broadleaf forest’ and ‘Mixed forest’ were extracted from the database. Landscape metrics were estimated by extracting patches found within dispersal distance [arbitrarily set to 5 km, according to average distance flight ability in several bark-beetle species estimated in flightmill (Forsse 1989)] from the sampling site, and by estimating the total area (TlaCon), number of patches (NpCon), mean patch size (MpsCon) and total edge (TeCon) of these extracted patches. The choice of these metrics was based upon the following assumptions: i) a large habitat area, and a high number of patches within dispersal distance should favour species persistence by preventing local extinction resulting from stochastic fluctuations; ii) stand edges have been shown to be favoured by *I. typographus*, *P. chalcographus*

and to a lesser extent, by *T. piniperda* (the higher abundance of *T. piniperda* in stand edge was only observed when related to a higher amount of breeding material) (Peltonen 1999; Göthlin, Schroeder and Lindelow 2000; Peltonen, Heliövaara and Väisänen 1997). A high amount of edges in the landscape could thus lead to higher infestation levels; iii) high amounts of edges and patches should also favour overall connectivity from one habitat patch to another. In addition, four other parameters were estimated to test the hypothesis that a mixing of broadleaf and coniferous patches would result in lower infestations: the areas of broadleaf forest patches (TlaBro), the numbers of broadleaf forest patches (NpBro), the amounts of edges shared by coniferous and broadleaf patches (Edcb) and the amounts of edges shared by coniferous, broadleaf and mixed patches (Edcbm). These metrics were calculated using the Patch Analyst (Elkie et al. 1999) within ArcViewGIS 3.2 (Esri, Redlands, CA), or using custom programs developed using ArcViewGIS 3.2 macro language Avenue (Esri, Redlands, CA), when not available in the Patch Analyst (Edcb, Edcbm).

Using the Corine Landcover involved two sources of error. Firstly, the database is based on remotely sensed data collected before 1994, and the forest cover may have changed since that period. Secondly, coniferous patches are assumed to be composed of spruce or pine in the analysis of the *I. typographus* / *P. chalcographus*, and *T. piniperda* / *I. sexdentatus* systems respectively, whereas they may actually be made of all types of mixtures of other coniferous species. The Corine Landcover was the best surrogate data we could obtain at the national scale on the French forest cover, as no tree species-specific database exists at this scale. We assumed that these two sources of error were random and uniformly distributed throughout the country, that they should thus inflate the risk of type I error (rejecting a true hypothesis), and that relationships observed as significant with the Corine Land Cover should remain so with better data.

All variables measured on site or by GIS analysis are presented in Table 1.

Analysis

Analyses were carried out on 4 insect species out of the 12 species or categories in the database. These 4 species were selected for their geographical coverage,

Table 1. Site and landscape variables and their abbreviation.

Variable	Type	Units	Abbreviation
Site			
Ecological region	Factor	–	Ereg
Tree species	Factor	–	Tsp
Site aspect*	Factor	–	Asp
Site topography [#]	Factor	–	Topo
Slope	Covariate	degrees	Slp
Elevation	Covariate	m	Ele
Average tree age	Covariate	years	Age
Average tree height	Covariate	m	H
Average tree diameter	Covariate	cm	Diam
Proportion of undamaged trees [§]	Covariate	%	Undam
Proportion of wind-felled trees [%]	Covariate	%	Pws
Landscape (within 5km from sampling location)			
Total coniferous forest area	Covariate	km ²	TlaCon
Number of coniferous forest patches	Covariate	#	NpCon
Mean patch size (coniferous forest)	Covariate	km ²	MpsCon
Total edge (coniferous forest)	Covariate	km	TeCon
Total broadleaf forest area	Covariate	km ²	TlaBro
Number of broadleaf forest patches	Covariate	#	NpBro
Coniferous vs. broadleaf forest edge	Covariate	km	Edcb
Coniferous vs. broadleaf and mixed forest edge	Covariate	km	Edcbm

*8 categories with azimuth interval of 45; [#]1 : crest ; 2 : slope ; 3 : bottom of slope ; 4 : depression ; 5 : valley ; 6 : other; [§]Proportion of trees undamaged by the storm in the stand where sampled trees are located; [%]Proportion of wind-felled trees among the 5 sampled trees.

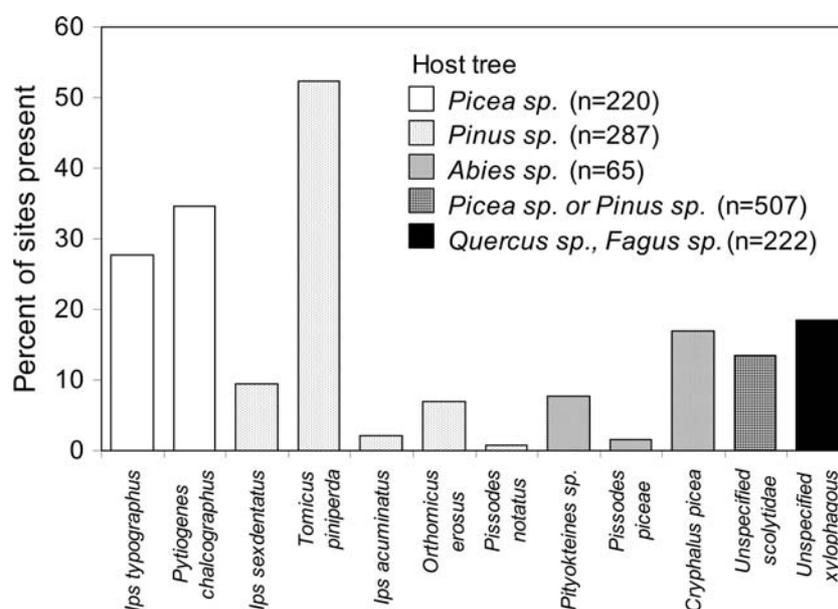


Figure 2. Proportion of sites where bark beetle and xylophagous species were observed during the spring 2000 survey.

frequency and relevance: *I. typographus* and *P. chalcographus* on spruce, and *T. piniperda* and *I. sexdentatus* on pine. *Ips acuminatus* and *Pissodes notatus* on pines were not selected because of their

low occurrence (Figure 2). *Orthotomicus erosus* was not selected because it is a Mediterranean species only observed in the southern sites of the study and was thus not suitable for the national scale analysis.

Species associated to *Abies* sp. were not selected because of the low number of site ($n = 65$) combined with the low numbers of observed individuals (Figure 2). Finally, the categories ‘unspecified scolytids’, and ‘xylophagous species’ were not selected because they may represent species having different ecological characteristics. Only the data from the first observation period of May – June 2000 are presented in this study, because its aim is to explore population patterns emerging straight after the storm, thus reflecting pre-storms population levels.

Spatial patterns in population estimates were analysed using standardized semi-variogram (Rossi et al. 1992). In presence of spatial structure, spherical models were fit to the standardized semi-variograms using a combination of fit-by-eye and least squares approaches and values for the scale, nugget, range and R^2 of the fit were obtained.

The spatial distribution of population density was analysed using geostatistical tools allowing the quantification of the statistical spatial dependence of sampling points replicated through space (Isaaks and Srivastava 1989). Statistical spatial dependence is important to the analysis of spatial datasets, first for the insight it provides on the variable under study when subject to interpretation (Rossi et al. 1992) and second 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).

The first step consisted in identifying variables significantly related to population estimates in a bivariate relationship. Population estimates were tested against covariates using Pearson’s correlation coefficient and against fixed factors using one-way ANOVA. Standard parametric tests of significance could not be used here because of SA that represents a bias to the assumption of independence among samples (Lennon 2000; Legendre et al. 2002). Using simulation data, Legendre et al. (2002) showed that Dutilleul’s modified t-test (Dutilleul 1993) constituted an efficient method to account for SA in estimating the significance of the correlation between two auto-correlated variables, and this method was used here to test the significance of all bivariate correlations. A Monte-Carlo approach was used to test the significance of the one-way ANOVA. Unconditional simulations of population estimates at sampling locations were carried out using a spherical model of the observed standardised semi-variance. These simulations generated 1000 distributions having population

estimate randomly distributed but spatially autocorrelated to the same degrees as the observed distribution. Simulated population estimates were tested against the factor value using one-way ANOVA and the distribution of the 500 F-statistics was used to test the null hypothesis. The factor effect was considered as significant (or highly significant) if the F-statistic calculated using observed population estimate was higher than the 95% (or 99%) percentile of the F-statistic distribution obtained with simulated data.

One general problem with correlation studies is the difficulty to determine if significant correlations reflect genuine ecological relationships, i.e., relationships that would persist in an independent data set. To address this issue, the analysis was stratified by large-scale ecological regions [defined as large-scale region with homogeneous forest and landscape characteristics (Nageleisen 2002a)] and fixed factors and covariates effects were compared across regions. A relationship was considered as genuine if it was found significant in at least one ecological region and if it showed a similar sign in the majority of the other regions.

In a second step, the factors and covariates considered as genuine were introduced into a GLM analysis in order to i) assess how much of the variability could be explained at the national level by the different factors and covariates, ii) explore how ecologically close variables (e.g., tree height vs. tree diameter) would co-exist in a single model, and iii) quantify SA in the model residuals to check if the spatial structure of population level estimates had been accounted for by the factors and covariates. A backward removal procedure was used to build the GLM. First, all variables were forced into the model. The factor or covariate that accounted for the lowest reduction in deviance (F-ratio test with $\alpha = 0.05$) was then removed from the model. This step was repeated until all factors or covariates remaining in the model were significant at $\alpha = 0.05$. Residuals of these GLM showed similar levels of SA as raw infestation levels and may therefore have biased parameters and significance. However, this was not too much of a concern here as the aim of the linear model was not to estimate variable parameters to allow unbiased predictions, nor a problem for inference as only significant and genuine bivariate relationships had been firstly included in the model.

Spatial and statistical analysis carried out using the number of infested trees per site (0 to 5) or the number of infested tree sections per site (0 to 30) as surrogate

population estimate provided very similar results, and these two variables were strongly correlated (*I. typographus*: $r = 0.931$; *P. chalcographus*: $r = 0.860$; *T. piniperda*: $r = 0.882$; *I. sexdentatus*: $r = 0.919$). As the numbers of infested tree sections had much stronger variance/mean relationships and showed strong evidence of heteroscedasticity in the GLM, we present only our analyses based on the number of infested trees per site.

Statistical analyses were performed using SPSS 11.5.1 (SPSS Inc., Chicago, Illinois, USA), modified t-test were estimated using Modttest (Dutilleul 1993), and spatial statistics were carried out using Surfer 8.0 (Golden Software Inc, Golden, Colorado, USA)

Results

Spatial analyses of the numbers of infested trees per site regardless of the insect or host tree species involved showed a clear positive spatial autocorrelation over long distances (Figure 3 a). This general result filters out the diversity of results obtained for each category (Figure 3b to f). *I. typographus* and *P. chalcographus* showed a weak spatial dependence (as measured by the nugget > 0.75) occurring over long distances (as measured by a long range of 186 and 158 km respectively). In contrast, *T. piniperda* showed a much stronger spatial dependence (nugget = 0.538) occurring at a much shorter range (38 km), whereas the spatial distribution of *I. sexdentatus* appeared to be random (i.e., a 'pure nugget' standardised semi-variogram).

I. typographus and *P. chalcographus* showed a similar geographical distribution (Figure 4): the highest infestation levels were observed in the north-eastern mountains (NEM) and very few stands showed signs of infestation in the Massif Central (MC), and north-west plains (NWP). In contrast, *T. piniperda* was present at various levels in all geographical areas where it was sampled. Highest population levels were observed in NWP where almost all sampled sites were found to be infested (Figure 3d and Figure 4). MC and south-western plains (SWP) had lower infestation levels and the north-eastern plains (NEP) and NEM had intermediate infestations levels (Figure 4). *I. sexdentatus* was found at very low levels in all ecological regions.

Bi-variate relationships between infestation levels and site, stand and forest cover characteristics showed contrasting results according to species study systems

(Table 2). Population levels in *I. sexdentatus* showed no significant relationship to any variable. *P. chalcographus* and *T. piniperda* showed a negative correlation with the proportion of wind-felled trees, i.e., a positive correlation with the proportions of wind-broken trees. A positive correlation was observed in *I. typographus*, *P. chalcographus* and *T. piniperda* with the proportions of undamaged trees. Infestation levels in *I. typographus* and *P. chalcographus* were positively correlated with average tree age and elevation. Infestation levels by *I. typographus*, *P. chalcographus* and *T. piniperda* were positively correlated with the numbers of coniferous patches. Finally, several factors were found significantly correlated to one single species group such as the slope (*I. typographus*), and length of edges shared by coniferous, broadleaf and mixed forest patches (*T. piniperda*). When entered into the GLM analysis, equivalent results were observed except that some variables were not incorporated into the model because of the presence of an ecologically-related variable accounting for a larger reduction in deviance (Table 3). Two species (*P. chalcographus* and *T. piniperda*) showed a significant effect of the ecological region in presence of the covariates. The proportion of undamaged trees was positively related to infestation levels by *I. typographus*, *P. chalcographus* and *T. piniperda*, whereas the proportion of wind-felled trees was negatively related to infestation levels by *P. chalcographus* and *T. piniperda*. In addition to these relationships, *I. typographus* infestation level was positively related to tree age, *P. chalcographus* and *T. piniperda* infestation levels were positively related to the number of coniferous patches in neighbourhood, and *T. piniperda* infestation level was negatively related to the length of edges shared by coniferous and broadleaf forest patches. Standardised residuals of the 5 groups GLMs showed similar levels of SA as the raw infestation levels (Figure 3) indicating that the spatial structure observed in the infestation data was not accounted for by the ecological region or covariates. An additional GLM was tested, in which the infestation level of the four species (*I. typographus*, *P. chalcographus*, *T. piniperda*, *I. sexdentatus*) attacking coniferous trees were pooled together (using the maximum summarising function for species observed on the same host tree species) and tested using a backward removal analysis with variables significant in each of the four systems. We observed a highly significant relationship with ecological regions ($F_{5,365} = 8.106$; $n = 375$; $p < 0.001$), with the proportion of

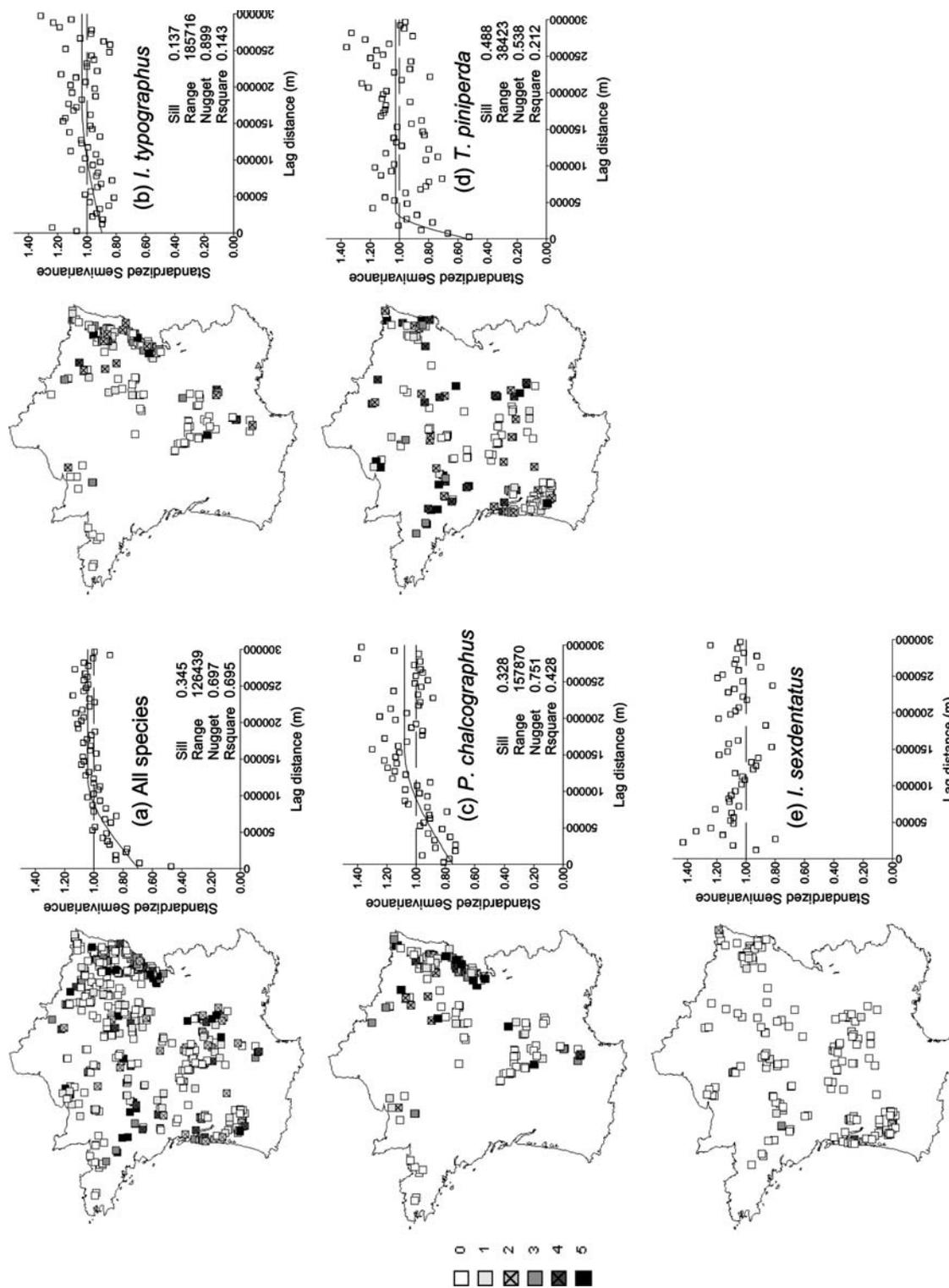


Figure 3. Distribution of the infestation level (0 – 5) by bark beetles regardless of host tree species (a); by *Ips typographus* (b) and *Pityogenes chalcographus* (c) on spruce, *Tomicus piniperda* (d) and *Ips sexdentatus* (e) on pine, observed at the first time period (March – July 2000) and their experimental standardized variograms (lag interval 10 km) and best fit models when spatial autocorrelation was observed.

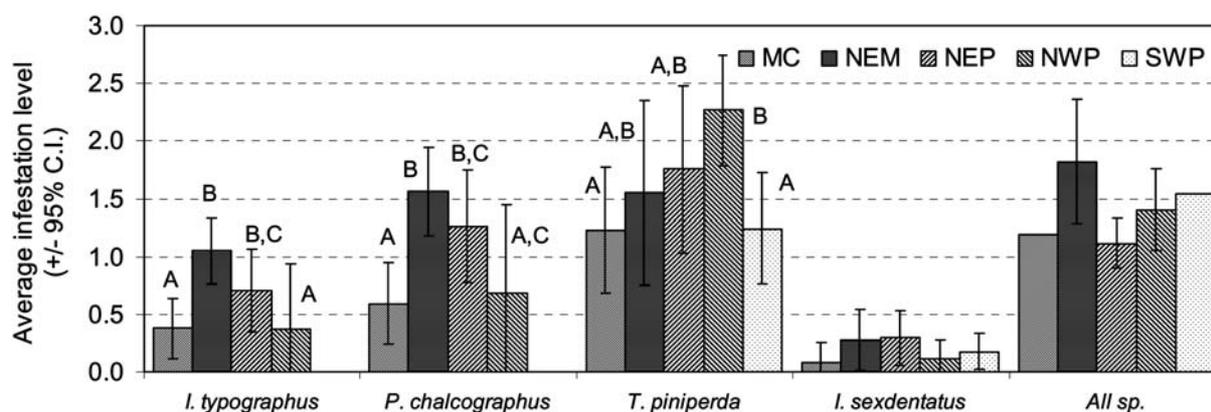


Figure 4. Regional effect on the infestation level for the four groups studied and for all species regardless of the infested host tree.

wind-felled trees (Pws; $F_{1,365} = 31.873$; $p < 0.001$), the proportion of undamaged trees (Undam; $F_{1,365} = 26.436$; $p < 0.001$), as well as a highly significant positive correlation to the number of coniferous patches (NpCon; $F_{1,365} = 18.257$; $p < 0.001$) and a highly significant negative correlation to the amount of coniferous/broadleaf edges in the neighbourhood (Edcb; $F_{1,365} = 6.967$; $p = 0.00865$). The overall model was highly significant ($F_{9,365} = 11.138$; $p < 0.001$) and accounted for 21.5 % of the variability.

Discussion

An intriguing result of this study was the presence of large-scale patterns in infestation levels, i.e., the fact that different species exhibited different levels of spatial autocorrelation (SA), together with differences in population sizes according to the ecological regions. SA was still present in the linear model residuals, indicating that the ecological regions, or other significant covariates, were not the main origins of the observed spatial patterns. Large-scale population synchrony (process by which spatially disjoint populations fluctuate in a parallel fashion) may produce large-scale autocorrelated population patterns such as reported in several forest insect pests (Peltonen et al. 2002 and ref. therein). However, we only had here an instantaneous view, a snapshot, of population levels, and therefore we do not know if the observed patterns would be stable in time (e.g., NEM would always be more infested by *I. typographus* and *P. chalcographus* than the MC), or if it is the result of large-scale population synchrony with populations fluctuating in a similar fashion within ecological regions (i.e., in a

disjoint way between ecological regions), in which case this pattern could change in the future (e.g., MC may in turn present higher infestations than NEM). Several factors not tested here may influence bark-beetle population levels at the regional scale: the distribution of past storms, large-scale climatic variations (e.g., temperature or rain), large-scale difference in the structure of the forest cover, or even regional differences in IPM strategies (see for example Perkins and Matlack 2002). Two storms affected France in the last 10 years before 1999 (Météo France 2003a): the February 1990 storm struck northern France, and the February 1996 storm hit only the south-west. The combined distribution of these two storms does not overlap with any part of MC, which could explain the presently lower levels of *I. typographus* in this region, whilst the latest important outbreaks were recorded there after a local storm in 1982 (Abgrall and Schvester 1987). Another candidate factor presenting large-scale variations is temperature, which is much milder in the western part of France close to the Atlantic ocean (average number of frost days ranging from 5 to 40, Météo-France 2003b) as compared to the Massif Central (50 to 90 days), or the north-west (60 to 97 days). Another example is the distribution of forest patches, which differs greatly from one ecological region to the other in term of size, abundance, overall fragmentation and broadleaf/coniferous level of mixity (Figure 1 B and C). Although it is reasonable to believe that these factors may contribute to structure populations at large-scale, complementary data allowing to test specific hypotheses regarding their effect would be required to allow further inference. The spatial patterns revealed here allow targeting areas with contrasted population levels

Table 2. Relationship between the infestation level and site, stand and forest landscape characteristics. To account for SA, the significance of the relationship with fixed factors was assessed by a Monte-Carlo procedure, and the significance of the correlation with covariates was measured using Dutilleul (1983) modified t-test (***) $p < 0.001$, ** $p < 0.001$, * $p < 0.05$. Relationships considered as genuine and incorporated into the GLM analysis are indicated in italic.

Ereg	<i>P. chalcographus</i>										<i>T. piniperda</i>										<i>I. sexdentatus</i>									
	MC	NEM	NEP	NWP	MCNEM	NEP	NWP	MC	NEM	NEP	NWP	MC	NEM	NEP	NWP	MC	NEM	NEP	NWP	MC	NEM	NEP	NWP	MC	NEM	NEP	NWP			
N	74	63	39	16	74	63	39	16	39	18	22	51	51	39	18	22	51	51	39	18	22	51	39	18	22	51				
Factors																														
Tsp	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.			
Asp	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.			
Topo	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.			
Site Covariates																														
Slp	<i>0.127</i>	<i>0.055</i>	<i>0.345*</i>	<i>0.123</i>	0.173	0.119	0.190	0.071	0.067	0.510	0.219	0.135	-0.042	0.023	0.422	-0.138	-0.059	-0.139	0.023	0.422	-0.138	-0.059	-0.139	-0.115	0.458	0.265	-0.035	-0.137		
Ele	<i>0.362*</i>	<i>0.119</i>	<i>-0.072</i>	<i>0.492</i>	<i>0.195</i>	<i>0.174</i>	<i>-0.091</i>	<i>0.618*</i>	0.188	0.436	0.195	-0.268	-0.258	-0.115	0.458	0.265	-0.035	-0.137	-0.115	0.458	0.265	-0.035	-0.137	0.148	-0.014	0.200	-0.016	-0.070		
Age	<i>0.387**</i>	<i>0.286*</i>	<i>0.379*</i>	<i>0.965***</i>	<i>0.158</i>	<i>-0.108</i>	<i>0.387***</i>	<i>0.837***</i>	0.241	-0.150	-0.091	-0.345	-0.128	0.148	-0.014	0.200	-0.016	-0.070	0.148	-0.014	0.200	-0.016	-0.070	0.170	0.269	0.224	0.071	0.016		
Diam	<i>0.286*</i>	<i>0.287*</i>	<i>0.255</i>	<i>-0.410</i>	0.095	0.014	0.172	-0.222	0.135	-0.125	-0.129	-0.205	-0.148	0.170	0.269	0.224	0.071	0.016	0.170	0.269	0.224	0.071	0.016	<i>0.327*</i>	<i>-0.011</i>	<i>0.331</i>	<i>0.283*</i>	<i>-0.033</i>		
H	-0.067	0.221	0.288	0.119	-0.049	0.152	0.311	0.143	-0.184	0.141	0.054	0.034	-0.236	0.327*	-0.011	0.331	0.283*	-0.033	0.327*	-0.011	0.331	0.283*	-0.033	0.174	-0.324	-0.173	0.117	-0.042		
Undam	<i>0.137</i>	<i>0.263*</i>	<i>0.202</i>	<i>-0.030</i>	<i>0.043</i>	<i>0.304*</i>	<i>0.303</i>	<i>0.033</i>	<i>0.174</i>	<i>0.331</i>	<i>0.430*</i>	<i>0.309</i>	<i>0.195</i>	0.174	-0.324	-0.173	0.117	-0.042	0.174	-0.324	-0.173	0.117	-0.042	0.097	-0.222	0.122	0.049	0.072		
Pws	-0.101	-0.059	-0.086	-0.523	-0.338**	-0.357**	-0.180	-0.359	-0.382*	-0.535*	-0.286	-0.414**	0.489***	0.097	-0.222	0.122	0.049	0.072	-0.382*	-0.535*	-0.286	-0.414**	0.489***	0.097	-0.222	0.122	0.049	0.072		
Landscape Covariates																														
TlaCon	-0.029	0.096	0.171	0.482	-0.200	-0.011	0.295	0.607*	-0.040	-0.286	0.161	-0.506**	-0.006	-0.134	0.261	0.036	0.008	0.253	-0.040	-0.286	0.161	-0.506**	-0.006	-0.134	0.261	0.036	0.008	0.253		
NpCon	<i>0.096</i>	<i>-0.006</i>	<i>0.375*</i>	<i>0.210</i>	<i>0.172</i>	<i>0.008</i>	<i>0.510***</i>	<i>0.265</i>	<i>0.418**</i>	<i>-0.464</i>	<i>0.387</i>	<i>0.166</i>	<i>0.046</i>	0.061	-0.203	-0.028	0.056	-0.210	<i>0.418**</i>	<i>-0.464</i>	<i>0.387</i>	<i>0.166</i>	<i>0.046</i>	0.061	-0.203	-0.028	0.056	-0.210		
MpsCon	-0.027	0.139	-0.148	0.250	-0.170	0.076	0.032	0.337	-0.163	0.053	-0.286	-0.343*	0.025	-0.091	0.316	0.084	-0.062	0.322*	-0.163	0.053	-0.286	-0.343*	0.025	-0.091	0.316	0.084	-0.062	0.322*		
TeCcon	<i>-0.018</i>	<i>0.084</i>	<i>0.386*</i>	<i>0.375</i>	-0.137	-0.107	<i>0.459**</i>	0.466	0.110	-0.423	0.286	-0.480*	-0.067	-0.115	0.281	-0.047	0.064	0.049	<i>0.459**</i>	0.466	0.110	-0.423	0.286	-0.480*	-0.067	-0.115	0.281	-0.047	0.064	
TlaBro	0.027	-0.090	0.142	0.260	0.085	-0.025	-0.049	0.351	-0.210	-0.067	0.338	-0.263	-0.083	0.118	-0.411	0.234	-0.066	-0.176	-0.210	-0.067	0.338	-0.263	-0.083	0.118	-0.411	0.234	-0.066	-0.176		
NpBro	-0.146	0.006	-0.220	0.052	-0.260	-0.061	-0.273	0.056	-0.303	0.687	0.106	-0.046	-0.120	-0.143	0.105	-0.061	0.100	-0.187	-0.303	0.687	0.106	-0.046	-0.120	-0.143	0.105	-0.061	0.100	-0.187		
Edeb	<i>-0.078</i>	<i>0.011</i>	<i>0.397*</i>	<i>0.431</i>	-0.134	-0.173	<i>0.451**</i>	<i>0.549*</i>	<i>-0.448*</i>	<i>-0.474</i>	<i>0.439*</i>	<i>-0.380*</i>	<i>-0.045</i>	0.008	-0.320	0.025	-0.026	-0.090	<i>-0.448*</i>	<i>-0.474</i>	<i>0.439*</i>	<i>-0.380*</i>	<i>-0.045</i>	0.008	-0.320	0.025	-0.026	-0.090		
Edebm	<i>-0.124</i>	<i>0.057</i>	<i>0.441*</i>	<i>0.423</i>	-0.135	-0.164	0.501*	0.534*	-0.374	-0.423	0.384	-0.485*	-0.077	0.019	-0.200	-0.022	-0.008	-0.118	<i>-0.441*</i>	<i>0.423</i>	<i>0.384</i>	<i>-0.485*</i>	<i>-0.077</i>	0.019	-0.200	-0.022	-0.008	-0.118		

Table 3. GLM of infestation levels at the site level as a function of site and forest cover neighbourhood characteristics (fixed factor significance: *** $p < 0.001$, ** $p < 0.001$, * $p < 0.05$; covariates sign and significance: +++/--- $p < 0.001$, ++/-- $p < 0.01$, +/- $p < 0.05$).

	<i>I. typographus</i>	<i>P. chalcographus</i>	<i>T. piniperda</i>	<i>I. Sexdentatus</i>
GLM				
N	189	189	181	181
d.f.	2	7	8	1
F	21.498	8.936	11.154	4.254
p	< 0.001	< 0.001	< 0.001	0.041
R ²	0.188	0.254	0.342	0.023
Variables				
Ereg	n.s.	***	**	n.s.
Slp	n.s.			
Ele	n.s.	+		
Age	+ + +	n.s.		
Diam	n.s.			
H				+
Undam	+	+	+ + +	
Pws		- - -	- - -	
TlaCon			n.s.	
NpCon	n.s.	+ + +	+ +	
TeCon	n.s.			
Edcb	n.s.		- -	
Edcbm	n.s.		n.s.	

that would permit to test such hypotheses (e.g MC vs. NEM vs NWP for *Ips typographus* and *P. chalcographus*, or SWP vs. NWP for *T. piniperda*). A large proportion of the variability in observed infestation levels was local (at least below the lowest lag distance interval: < 5 km) as indicated by the relatively high nugget in the standardised semi-variograms. Variables summarising population levels at a larger scale than 5 trees per site (e.g., total number of infested trees per homogeneous patch) may prove more appropriate to explore relationship with large-scale structuring factors. However, French forests have been deeply influenced by man since the Neolithic: they have been subjected to intense fragmentation (see Figure 1 B and C) and often undergone repeated changes in composition and structure. Therefore, in comparison to the more extensive North American forests where large-scale influences on bark-beetle populations of factors such as elevation, climate, fire, drought or large-scale landscape mosaics have been observed (Coulson et al. 1999; Powers et al. 1999; Bebi, Kulakowski and Veblen 2003), these factors may not be good predictors for outbreaks in France, where local factors could have a greater impact on the variability. In particular, the management regime may change

drastically from one small stand to another located in the close vicinity, thus having a local and much profound impact on the risk of bark-beetle outbreak than large-scale spatial factors.

A significant proportion of the variability was thus related to local factors. Two factors were significantly related to population levels in multiple study systems: the proportion of undamaged trees (*I. typographus*, *P. chalcographus* and *T. piniperda*) and the proportion of wind-felled trees among the sampled trees (*P. chalcographus*, *T. piniperda* and xylophagous sp.). The positive relationship between population levels and the proportion of undamaged trees has not yet been observed in other studies. It can easily be interpreted by the dilution of the pre-existing populations among the available breeding material. If the population levels existing before the storm are proportional to forest size, a higher level of infestation is expected per wind-damaged tree if these are scarce. The negative relationships between population levels and the proportions of wind-felled trees among the sampled trees reflect the preference of the beetles toward wind-broken trees, which was already reported in local studies (Göthlin, Schroeder and Lindelow 2000). Wind-felled trees having part of their root still in

Table 4. Ecological characteristics of the studied species.

	<i>I. typographus</i>	<i>P. chalcographus</i>	<i>T. piniperda</i>	<i>I. sexdentatus</i>
Aggregative pheromone	+	+	–	+
Outbreak type*	Eruptive	Eruptive/Gradient	Gradient	Gradient
Size (mm)	4-5	2-2.3	3.2-5	6.2-7.8
Aggressiveness [#]	+++	+	+	+
Geographical extension [#]	+++	+++	+++	+++
Preference for forest edges [§]	+	+	+/-	?
Disruptive NHV [¥]	+	+	+	+

* Berryman (1986); [#]Lieutier et al. (2004): +: low, ++: medium, +++: high; [§] *I. typographus* and *P. chalcographus*: Peltonen 1999, Göthlin, Schroeder and Lindelow 2000; *T. piniperda*: Peltonen 1999; [¥] *I. typographus* and *P. chalcographus*: Byers et al. 1998, Zhang and Schlyter 2003; *T. piniperda* and *I. sexdentatus*: Poland and Haack 2000, Kohnle et al. 1992, Jactel et al. 2003.

contact with the soil are still partly alive and have kept some of their resistance at the time of the beetles' first emergences. This pattern is likely to reverse in the following year as observed by Göthlin, Schroeder and Lindelow (2000), when wind-broken trees would have completely dried out and when wind-felled trees may still be suitable for brood development. In this context, it is not surprising to see that apart from *I. sexdentatus* (see below), *I. typographus* was the only study system not showing preference toward wind-broken trees, as it is the species most prone to a primary attitude. Although it was not expressed by the same variables, *I. typographus* and *I. sexdentatus* positively correlated with factors related to tree size (respectively age and height), which has also been reported in other works for *I. typographus* in stands (Göthlin, Schroeder and Lindelow 2000; Jakus 1998) or mechanically created high stumps (Schroeder et al. 1999). *I. typographus* and *I. sexdentatus* are the largest species among those analysed in this study (Table 4), they generally infest the trunks and are therefore more likely to favour larger trees than the smaller *P. chalcographus* or *T. piniperda* that are able to exploit other niches such as top branches or stumps.

Relationships between landscape neighbourhood variables and infestation levels also showed different results for each study system. A positive relationship with the number of patches was observed in *P. chalcographus* and *T. piniperda* (and in *I. typographus* in a bivariate correlation relationship), whereas *T. piniperda* infestation levels showed a negative relationship with the amount of edges shared by coniferous and broadleaf forest patches. Although these relationships are in accordance with our hypotheses (infestation is favoured by high number of neighbourhood patches and low coniferous/broadleaf level of contact), we would have ex-

pected to find them in all study systems as these three species may all potentially benefit from the presence of host patches in the neighbourhood, and have been shown to have their host finding processes affected by NHVs (see Table 4, and refs. therein). Moreover, it is rather surprising not to observe a positive edge-effects in *I. typographus* and *P. chalcographus* as reported in local studies (Peltonen 1999; Göthlin, Schroeder and Lindelow 2000). One possible reason for the absence of broadleaf-shared edge effects in *I. typographus* and *P. chalcographus* might be the role of their aggregative pheromone (not present in *T. piniperda*, see Table 4) that would make these two species less sensitive to NHV disruption at the landscape scale. Another possible hypothesis, that also explains the absence of positive effect of coniferous edges, is that this positive effect may be counter-balanced by the negative effect of edges shared with broadleaf forest patches in *I. typographus* and *P. chalcographus*. This hypothesis is supported by the much less pronounced preference for forest edge reported in *T. piniperda* (Peltonen 1999) which would less counterbalance the negative effect of broadleaf-shared edge on infestation level, and make it measurable at the landscape scale. To test if this hypothesis is statistically realistic, we forced the variable Edcb into the GLM for *I. typographus* and *P. chalcographus* with the same parameter as in the *T. piniperda* model. These models residuals were found significantly positively correlated to the total amount of coniferous edge (respectively $p < 0.001$ and $p = 0.036$ for *I. typographus* and *P. chalcographus*), indicating that these two factors may indeed mask each other in these two species. Significant relationships (positive and negative respectively) with the numbers of coniferous patches and of broadleaf-shared edges emerge when

data from the four conifer bark-beetle species are pooled together; this further supports the suspicion that this pattern might be more general than suggested by the results in each individual study system.

As no significant relationship was found between the population level and the total coniferous landscape areas or the mean coniferous patch sizes, it is unlikely that the observed correlation with the number of coniferous patches simply reflects the higher abundance of host trees available within dispersal distance. This relationship is rather interpreted as the positive effect of the numbers of coniferous patches on the metapopulations persistence. Three main causes, demographic stochasticity, environmental stochasticity and host/parasitoids dynamics may lead bark-beetle populations to extinction, and make the metapopulations benefit from a high number of patches. Demographic stochasticity is unlikely to cause extinctions in bark beetles: these insects are generally found in high numbers (several thousands per infested tree) and have positive growth rates, which translates into a potentially unlimited time to extinction according to the simplest demographic models (constant growth model and Ricker model, Foley 1997). Environmental (or catastrophe) stochasticity (Foley 1997), especially when it consists in IPM measures directed toward infested trees, may possibly lead to local extinction. Actually, we have several reasons to believe that a constant residual population may persist even in intensively managed stands: infested trees are generally discovered only when most of the population has left the host tree, and the beetles do not require whole trees to develop, and may thus find enough breeding material (stumps, branches, logs) to persist in intensively managed stands. However, under this hypothesis, the bark-beetle metapopulation would be positively correlated to a higher abundance of host-trees (measured as the host tree cover area) in the neighbourhood, and not as we observe here, to the number of patches. High patch numbers could allow bark beetles to escape from their natural enemies: theoretical and experimental work demonstrates that high numbers of interconnected patches (and not necessarily their size) greatly favour metapopulation persistence in host/parasitoids systems (Nee, May and Hassel 1997; Hassel and Wilson 1997).

We interpret the negative correlation between population levels and the amount of edge shared by coniferous and broadleaf patches observed in *T. piniperda* as an effect of the NHVs' disruptive effect on the host-tree finding process, although

alternative hypotheses (such as for example more diverse and stable natural-enemy communities along broadleaf/coniferous edges) can be opposed to this semio-chemical-diversity hypothesis proposed by Zhang and Schlyter (2002).

I. sexdentatus showed no significant relationships with any of the factors studied except with tree height (at low significance), and was randomly geographically distributed. This apparently random pattern probably relates to the very low population levels (although the species was present in all ecological regions, cf. Figure 4) that does not allow the establishment of quantitative relationships. The reasons for such low level of endemic population are unknown, but it was observed that the species showed important secondary developments stemming from these apparently random first infestation (Nageleisen 2002b).

This study thus provides three main results: (i) the four most abundant conifer bark-beetle species present in France in 1999 displayed large-scale spatial patterns and geographical variations in abundance, and these variations are not related to the site, stand and landscape factors tested here (still present in the GLM residuals), but more likely to large-scale structuring factors such as climate or regional forest cover structure, (ii) the beetles dispersed among the available wind-damaged trees (hence lower infestation per tree were observed in stands with a high proportion of damaged trees), with a preference toward wind-broken trees, and (iii) bark-beetle populations showed significant relationships with the structure of the coniferous forest cover (in particular with the numbers of coniferous patches) and with the amounts of coniferous edges shared with broadleaf forest patches, which can be interpreted as the disruptive effect of NHV on host-finding process and provides a new argument in favour of the diversity-stability theory. The spatial and temporal scale of the present study is certainly not the most appropriate to test the disruptive effect of NHV at the landscape scale, nor to test the more speculative interpretation of patch number effect on host/parasitoid metapopulation persistence. Establishing and quantifying such effects at the landscape scale is difficult because one can hardly manipulate a whole landscape according to an *a priori* experimental design. Our results call for field studies following population levels using individual stands as sampling units, conducted at a spatial scale closer to the scale at which these processes occur (100–200km wide areas), maintained for several years in a region

including a variety of patch sizes, shapes, densities and levels of interconnection with broadleaf forest, such as to better assess the effect of NHV and landscape structure on bark-beetle populations.

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