

Occurrence of *Ips typographus* (Col., Scolytidae) along an urbanization gradient in Brussels, Belgium

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- Abstract**
- 1 The distribution and dynamics of insect populations in cities is poorly understood. One approach to address this question is to explore the permeability of the urban habitat to species from surrounding rural areas, which can serve as reservoirs in source-sink dynamics.
 - 2 Here, we present data on the distribution of the forest insect pest of spruce, *Ips typographus* (Coleoptera, Scolytidae), along two axes entering the city of Brussels (Belgium) from the south-east and to the town centre.
 - 3 The insect was caught everywhere along these transects, even in heavily urbanized surroundings, and sometimes in relatively high numbers. The catches were highest near the middle of the transects and lower at both ends of them.
 - 4 This pattern was associated, on the one hand, with an urbanization gradient with the numbers of flying individuals increasing with the distance from the city centre and, on the other hand, with lower catches at the periphery of the city where a high proportion of broadleaved trees may have disrupted the response to aggregation pheromones.
 - 5 In addition to the probable rural origin of the beetles, high catches at the Port of Brussels indicated that some of the insects might be of foreign origin and enter the city with imported timber, highlighting a pathway for unintentional introductions of organisms, including potentially invasive species.

Keywords Bark beetles, invasive species, *Ips typographus*, nonhost volatiles, pheromones, *Picea abies*, urban ecology.

Introduction

Urban ecosystems correspond to areas under intense and constant human activity, composed of high-density human habitation, industries and remnants of seminatural habitat (McIntyre *et al.*, 2001). These ecosystems are spatially heterogeneous and temporally dynamic, differing from their rural surroundings and from previous conditions by a greater coverage of impermeable surfaces, higher air, water and soil pollution, and by a specific microclimate. According to Rebele (1994), there are also higher numbers of exotic species, especially plant species, in urban environments than in rural conditions. Because of the scarcity and

low quality of suitable habitats, we can assume that the persistence of many species is highly dependent on the flow of individuals entering the cities (Davis, 1982). This flow depends on the dispersal mechanism (active or passive) and on the city-landscape patchwork in which it is taking place. We were particularly interested in exploring the permeability of such a patchwork to species actively dispersing from a rural population reservoir. Although several studies have described the distribution of wildlife species in cities (Kozlov, 1996; McIntyre *et al.*, 2001; Zerbe *et al.*, 2003), very few studies specifically concentrated on their penetration pathways, and on the impact of urban environment on the flow of species towards city centres. Moreover, the influence of landscape type, such as buildings or vegetation composition, on dispersal is still an unexplored research area.

In previous experiments (unpublished), the forest insect pest *Ips typographus* (L.) (Coleoptera, Scolytidae) was unexpectedly caught in pheromone traps in Brussels. This pest of

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spruce (*Picea abies* L. Karst) is distributed throughout Eurasia and caused the loss of 31 millions cubic metres of spruce in western and central Europe between 1990 and 2001 (Grégoire & Evans, 2004). It is considered as one of the most damaging forest insects in Europe. However, although they can be commonly observed in boreal cities surrounded by spruce forests, damage caused by *I. typographus* is rarely reported in cities in western Europe, such as Brussels, probably because the scarcity of hosts does not allow populations to grow to a damaging level.

This species therefore constitutes an excellent indicator to study the permeability of the city to flying insects. Furthermore, *I. typographus* can be trapped easily with synthetic aggregation pheromones (Bakke, 1977; Nilssen, 1984) that are used to bait small and cheap traps. *Ips typographus* flights appear to be generally quite short but they are able to cover several kilometres (Botterweg, 1982; Nilssen, 1984; Forse & Solbreck, 1985). According to Botterweg (1982), the species could spread over more than 8 km out of a forest area, and this would potentially allow some individuals to reach the centre of cities by flight, but little is known on the proportion of a population source that may migrate over such long distances. Moreover, it cannot be excluded that some small populations could be present within Brussels, depending upon the presence of local spruce trees or to small stocks of firewood. By analysing the distribution of *I. typographus* catches in pheromone traps disposed along two transects entering the city of Brussels in 1999 and 2000, this study aimed to explore the variability in populations in relation to: (i) a gradient from the rural area to the city centre and (ii) the structure of the urban landscape along the transects.

Materials and methods

Study area

The research was carried out in the south-eastern part of Brussels. The city has a population of approximately one million inhabitants and covers an area of 161 km², which corresponds to an average density of 6309 inhabitants per square kilometre (INS, 2003). Even if this density is relatively high, the number of urban green spaces in Brussels is also very high. The open (nonbuilt up) spaces in Brussels cover more than 8500 ha, which is approximately half of the Region's area (Gryseels, 2003). The biggest green space is the Sonian forest, an ancient forest composed of 85% of beech trees (*Fagus sylvatica* L.). It extends over an area of 4383 ha, of which 1654 ha are included within the administrative limits of Brussels. A wooded park, the 'Bois de la Cambre', extends this forest and allows the green spaces to penetrate very deeply into the city (Fig. 1).

From a structural point of view, three different concentric zones from the town centre to the outskirts are usually employed, corresponding to the historical spread of the city (Fricke & Wolff, 2002): (i) the highly urbanized centre with very few green spaces and many small very densely built blocks; (ii) the 'first crown' with a greater amount of green spaces, mainly with adjoining buildings

and an intermediate density of urbanization; and (iii) the 'second crown' with many green spaces and gardens, bigger blocks with non-adjoining houses and a relatively low density of urbanization compared with the city centre. According to this structure, we calculated the area covered by vegetation and by buildings for each zone. These proportions are 10% and 68% in the centre, 35% and 47% in the 'first crown', 70% and 16% in the 'second crown', respectively. Our study area mainly extended to the two intermediate zones (i.e. first and second crown).

We also set up traps near the port of Brussels, in the north central part of the city. Even if this site is located in the 'second crown' (Fig. 1), its land-use characteristics are closer to those of the city centre. Indeed, even if the area covered by buildings in the surroundings of the traps is relatively low, it is mainly a mineral industrial environment with an almost total absence of vegetation.

The distribution of *I. typographus*' main host-tree *Picea abies* is highly scattered in Brussels. No census data exist about the distribution of spruce in the administrative limits of the city, and it was very difficult to obtain a comprehensive census of spruce distribution within the framework of this study due to the fragmentation and private property of the urban landscape. Although Brussels is a rather green city (Fig. 1), spruce trees are particularly rare and are only found as isolated trees in private gardens, or as small groups of trees in parks and public gardens. During preliminary surveys in parks and public gardens, only three small patches of mixed conifers, including a high proportion of spruce (> 40%), could be found, in the south-western part of the Sonian forest, in the eastern part of the Sonian forest, and in the Parc de la Woluwe. Apart from such groups of trees, some isolated trees may be found in private gardens, but this is particularly difficult to census at the scale of the city because private gardens are generally within building blocks (i.e. behind buildings and not visible). The only way to locate spruce trees was via the interpretation of aerial photographs, and this was carried out in the vicinity of our sampling locations (see below). Outside Brussels' limits, 78 spruce patches are known in a radius of 12.5 km from the city centre, mainly in the south-east (Fig. 1). Their average size is 0.6 ha and the maximal extent is 3 ha. The closest important spruce plantations are located approximately 50 km to the south-east. Spruce attacks or damage caused by *I. typographus* were never reported in Brussels.

Data

Quantitative assessment of *I. typographus* populations entering the city was performed with pheromone traps distributed along two transects (Fig. 1). The first transect started from the Sonian forest and ended in the first crown, following the main railway line connecting Brussels to the spruce-rich south-eastern part of the country (this transect is termed 'railway transect'). The second transect was set up across the urban network, running across parks, housing blocks and private gardens, from the Sonian forest to the Leopold district (transect termed 'block transect'). Both transects were approximately 6 km

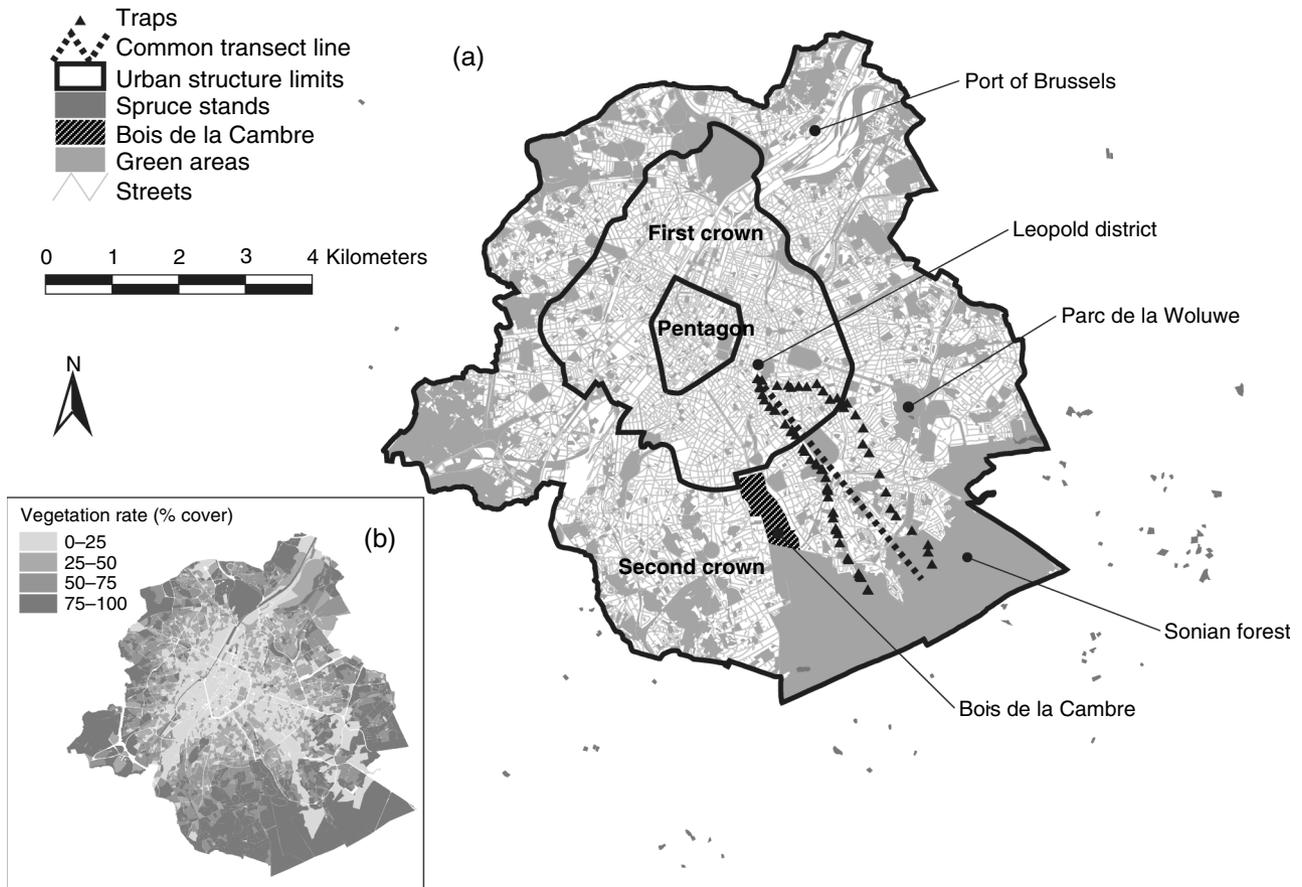


Figure 1 (a) Location of *Ips typographus* traps in 2000 and urban structural zones in Brussels (Belgium). (b) Vegetation rate (% cover).

long. Each 30×15 cm 'bottle-trap' (Franklin *et al.*, 2000) disposed along these transects was baited with a Pheroprax[®] dispenser (Cyanamid Agro, Belgium), and placed at a height of approximately 1.5 m on tree trunks in the forest, parks, private gardens, railway embankments or along green lanes. Because of the scarcity of the host and to avoid risk of attack, traps were not placed on spruce. The two transects were composed of 43 traps in 1999 and 63 traps in 2000. One trap was set up in each site, with an average distance of 217 m ($s = 147.48$ m) between two traps.

The first trapping campaign covered the second flight of the bark beetle and was carried out from August to October 1999. The traps were collected a first time an average of 22 days after set up and a second time 35 days after the first collection. The average total duration of trapping was 57 days in 1999. The second trapping period extended from April to July 2000 during the first, and generally more abundant, flight of the insects. We collected the traps, first, on average 28 days after placing the traps and, second, 41 days after the first collection. The average total duration of trapping was 69 days in 2000.

At the end of the second campaign, two traps were added near the port of Brussels, in the north-central part of Brussels, to test the hypothesis that some individuals may

enter the city centre with spruce logs (approximately $150\,000\text{ m}^3/\text{year}$) imported from Russia and the Baltic States. These two traps were laid during a much shorter period than the other traps (approximately 15 days). In addition, the imported timbers were inspected for bark-beetle presence. Some individuals and the typical patterns of galleries of *I. typographus* were observed.

The percentage of building area (*Bu*), the percentages of area covered by broadleaved trees (*Br*) and by conifers (*Co*), and the number of spruce (*Su*) were estimated within a radius of 200 m around each trap using visual interpretation of aerial photographs (colour aerial photographs of Brussels in 1996 at a scale of 1 : 4000). Land-use data extracted from the National Geographic Institute land-use database were used to validate the estimates of the percentage of building area and the percentage of area covered by broad-leaved trees, and showed very significant levels of correlation (bilateral Pearson correlations were all significant at the 0.01 level of probability).

Analysis

Insect count data are known to present strong proportionality between local mean and variance, and a highly

left-skewed frequency distribution, far from normality (Taylor, 1961). This was the case with our trap catches and these data were thus log-transformed [$\log_{10}(x + 1)$] to reduce the proportionality between mean and variance and to normalize the frequency distributions.

Spatial autocorrelation in log-transformed trap catch data was quantified with standardized variograms (Rossi *et al.*, 1992). Quantifying spatial autocorrelation was important because of the insight it may provide on the studied variable (Rossi *et al.*, 1992) and because the presence of spatial autocorrelation represents a bias to the assumption of independence among samples, which needs to be taken into account in parametric statistical analyses such as linear models (Lennon, 2000).

We found no evidence of spatial autocorrelation in our data, and this allowed us to use a standard Generalized Linear Model (GLM) to test the effect of years and covariates on log-transformed catches of *I. typographus*. First, all variables were forced into the model: the fixed factors year (year) and transect (*Tr*: railway transect; block transect), the covariates *Bu*, *Br*, *Co* and *Su*, and the distance to the city centre (*Di*; to analyse and compare transect data as a function of distance to the city centre, both transect locations were projected on a common transect line; see Fig. 1). 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 $\alpha = 0.05$. Visual examination of the plots illustrating the relationships found with the GLM modelling approach suggested a shift in the relationship between log-transformed trap catch data and the proportion of area covered by buildings (*Bu*) before and after 4200 m from the city centre. A second model was therefore built to test if the relationship between log-transformed trap catches and *Bu* was statistically different before and after this distance limit. An additional fixed factor having different values before and after 4200 m (*Dli*) was thus introduced in the GLM model and tested as a main factor, and by interaction with the proportion of area covered by buildings (*Bu*).

Results

The number of bark beetles caught, average number of insects per trap and standard deviations, and ranges of catches per trap for both trapping campaigns are summarized in Table 1.

The two traps near the port of Brussels caught, respectively, 115 and 170 individuals in 2000, which is proportionally very high compared with the other traps because these two traps were laid during a much shorter period. The average catches per day were 9.5 *I. typographus* near the Port of Brussels and 0.4 individuals in other locations.

The exploratory variography using standardized variograms showed no spatial dependence of the trap catches along the transects neither in 1999, nor in 2000. Both standardized semivariograms showed 'pure nugget effect' (i.e. values varying around an horizontal line at 1), which reflects an absence of spatial autocorrelation. The GLM analysis indicated that there was no significant effect of the transect type, proportion of area covered by coniferous trees, number of spruces, and distance to the centre, on the log-transformed trap catch data. We found a significant difference between the two years, and a significant association with the proportion of area covered by buildings (Table 2, General model). The plot of *I. typographus* trap catch data as a function of these two variables (Fig. 2) confirmed this trend, but highlighted a structural change along the transect. Within a distance of 4200 m from the centre, the moving-window average lines of trap catch data were revealed as the mirror image of the proportion of area covered by buildings (grey bold line vs. black bold line), suggesting a strong negative association. By contrast, beyond this distance limit, no such pattern was visually obvious. This effect was statistically confirmed in the GLM model (Table 2, Model by zone), with a highly significant interaction term between the transect zone (zone 1 < 4200 m, zone 2 > 4200 m) and the percentage of area covered by buildings, reflecting a shift of the relationship between *I. typographus* trap catch data and this variable before and after this distance limit (Fig. 3).

Discussion

Our study provides four complementary results. First, a typical forest insect pest is found everywhere along our transects, even in a heavily urbanized environment, and this implies that this species is able to disperse in areas where the host-plant is particularly rare, and exploit scarce and isolated resources. Second, in the highly urbanized centre (i.e. for distances less than 4200 m from the city centre), the distribution of insect catches responds to structural changes in the city, implying that the dispersal of the insect or the distribution of small local populations are affected by the urban structure. Third, we find a shift in the relationship with

Table 1 Summary of the results of the trapping campaigns of 1999 and 2000: number of traps, number of *Ips typographus* caught, average number of *I. typographus* per trap and standard deviation, maximum and minimum of catches per trap

Site	1999					2000				
	<i>n</i>	Catches	Mean \pm SE	Max	Min (<i>n</i>)	<i>n</i>	Catches	Mean \pm SE	Max	Min (<i>n</i>)
Railway transect	21	99	4.7 \pm 6.0	24	0 (3)	38	1092	28.7 \pm 30.3	123	0 (2)
Block transect	22	50	2.3 \pm 3.2	11	0 (9)	25	606	24.2 \pm 41.8	188	0 (3)
Transects	43	149	2.8 \pm 4.2	24	0 (12)	63	1698	28.4 \pm 38.8	188	0 (5)
Port of Brussels	–	–	–	–	–	2	285	142.5 \pm 38.9	170	115 (0)

Table 2 Results of the GLM model of log-transformed *Ips typographus* trap catch data as a function year (year) and transect type (*Tr*), percentage of building area (*Bu*), percentages of area covered by broadleaved trees (*Br*) and conifers (*Co*), and the number of spruce (*Su*) within radius of 200 m

Model	r^2	n	P	Effect	d.f.	F	P
General model	0.271	106	< 0.001	year	1	28.37	< 0.001
				Bu	1	12.94	< 0.001
Model by zone	0.397	106	< 0.001	year	1	7.24	< 0.001
				Bu	1	5.85	0.017
				Dli	1	15.97	< 0.001
				Dli × Bu	1	17.36	< 0.001

The general model includes main effect found significant at the end of the backward removal step by step procedure. The model by zone includes an additional fixed factor (*Dli*) dividing the transect in two zones, before and after 4200 m from the city centre, and tests its interaction with the percentage of area covered by building

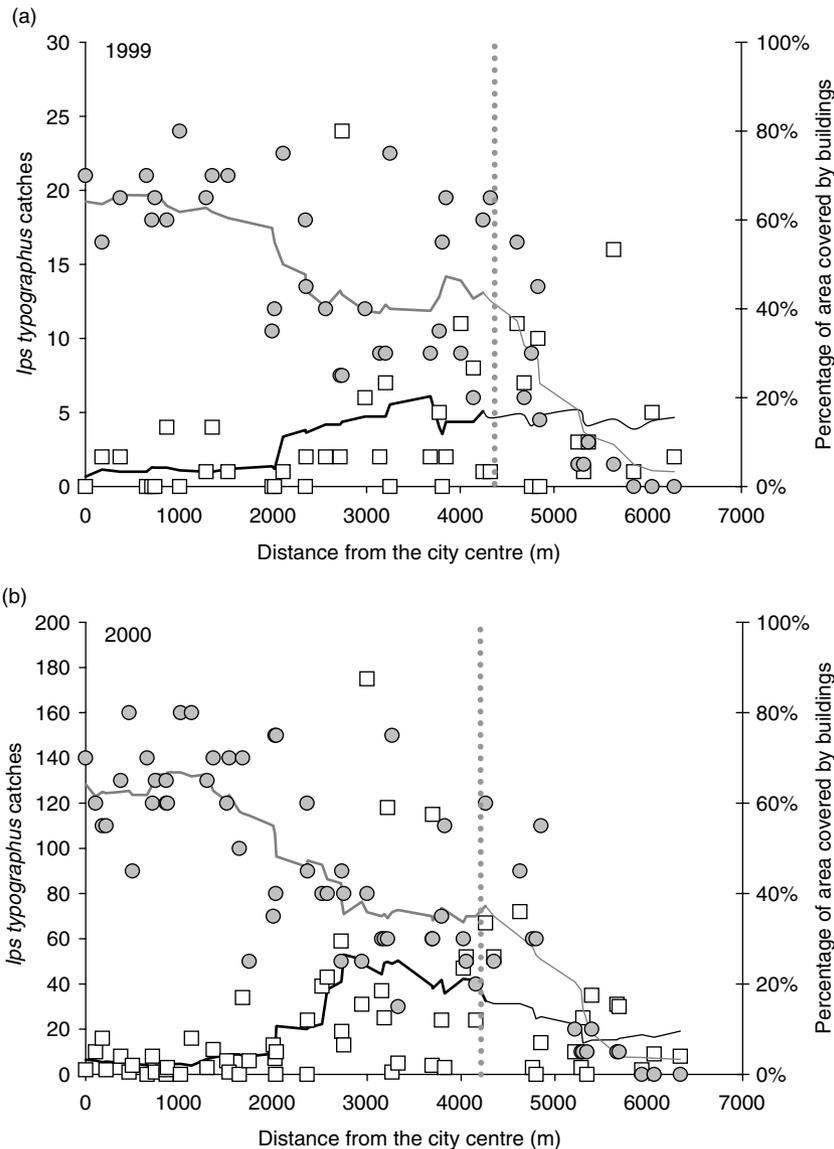


Figure 2 Distribution of the *Ips typographus* catches data (white squares) and percentage of building area (grey circles) and their moving-window average lines (11 points; black and grey line, respectively) as a function of the distance from the city centre (metres) before (bold) and after (normal) the limit of 4200 m (vertical grey dotted line). These two lines are the mirror image of each other along an horizontal axis before 4200 m (inverse relationship), and this pattern appears to change after this distance limit.

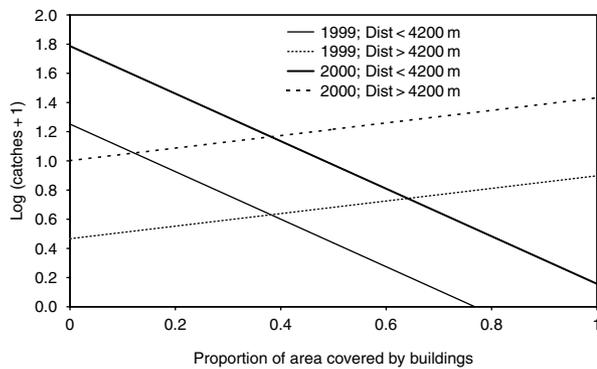


Figure 3 Predicted values of log-transformed *Ips typographus* trap catch data as a function of the proportion of area covered by buildings before and after 4200 m from the city centre, and for the years 1999 and 2000.

building density when the transects enter the Sonian forest, mostly composed of broadleaved trees, and we interpreted this as a possible disruptive effect of nonhost volatiles (NHVs) on trap efficiency. Fourth, traps located in the port of Brussels caught comparatively more insects than expected from their location and surroundings (mostly dense urban), suggesting that these populations may have been introduced with imported spruce timber, thus highlighting the role of trade as a potential pathway for invasive species.

Under the assumption that cities constitute an unfavourable environment, relatively far from *I. typographus*' natural host habitat, and even if they are lower than trap catches in forest areas, the catches in Brussels indicate that the number of individuals can be relatively important. The difference among the catches between the two years of study (both in general and by zone models) is probably mainly related to the difference between the trapping periods. In 1999, we focused on the second flight whereas, in 2000, we caught insects from the first flight, which corresponds to the first bark-beetle emergence, when they respond particularly well and synchronously to pheromone trapping. The very fact that *I. typographus* was caught almost everywhere indicates an ability to reach and potentially exploit very scarce and isolated resources, and suggests that every spruce in the country could be attacked if it became vulnerable (e.g. because of a climatic stress). This might suggest that forest insects such as *I. typographus* could fly further in an urban environment than in a forest of suitable hosts, although there is the need to be sure of the origin of the caught beetles before this hypothesis can be confirmed.

There was an inverse relationship between log-transformed catches and the proportions of building areas (Table 2; General Model), and this relationship was the strongest before the distance limit of 4200 m (Table 2; model by zone). The overall inverse association probably simply reflects the overall centre-periphery increasing population gradients, whereas the close and tighter response (Fig. 2) would result from the changes in direct accessibility to the traps with increasing building density. A high building density involves more dense physical local barriers, such as walls or building blocks. These may have a direct impact on trap

accessibility by flight, but also affect the diffusion of the pheromone with local whirlwind or canyon-effects, and hence influence the insect's ability to find the trap by its pheromone signal. These effects could locally prevent the insects distributed within the attraction range reaching the trap, and explain the close response to structural changes in the city (e.g. the change in the urban density associated, both in 1999 and in 2000, with the significant decrease in catches around 2000 m from the city centre, corresponding to the limit of the 'first crown'). The combined effect of large-distance, centre-periphery gradient and short distance trap accessibility would also explain why this variable comes first, before the distance to the city centre in the linear model. The effect of trap accessibility (physical or chemical through perturbation on wind flows) on catches may also explain why so little spatial dependence in the trap catch data was observed because trapping conditions affecting traps accessibility are typically spatially heterogeneous. In addition, the fact that the transect data were so spatially similar (see the 2-year transect moving-window average of 1999 and 2000, Fig. 2) suggests that they depend on a factor that remained unchanged between those 2 years, such as the spatial structure of the buildings. It cannot be excluded that some variation may also relate to changes in the distribution of local resources. However, first, no such source (e.g. infested spruces or stocks of firewood) could be identified in the field, even after thorough searches within the surroundings of traps with the highest catch numbers, and, second, these sources would probably have changed from one year to another, and would have resulted in different distribution patterns, which we did not observe.

We observed a shift in the response to the urban gradient beyond the distance limit of 4200 m. In other words, catches started to decrease significantly, or showed much lower levels than expected from the expected overall urbanization gradient, when the transect entered the broadleaved Sonian forest. This distance corresponds to an important increase in the proportion of broadleaved trees in the area (whilst conifer density remains stable). This pattern is interpreted as the possible disruptive effect of nonhost volatiles on the response of bark beetles to aggregation pheromones. It has been found that NHVs emitted by broadleaved tree species, such as birch, poplar or ash, have a clear repulsive effect on the response of many bark beetles to pheromones (Byers *et al.*, 1998, 2000; Zhang *et al.*, 1999a; Zhang & Schlyter, 2003). Such a repulsive effect would be efficient only from a high proportion of broadleaved trees in the surroundings of the trap. (Z)-3-hexenol was identified as one of these compounds (Byers *et al.*, 1998) and is one of the main volatiles emitted from the leaves of beech (Tollsten & Müller, 1996), the dominant species in the Sonian forest. A greater emission of NHVs in spring than in late summer due to maturation of leaves is also likely (Zhang *et al.*, 1999b; J. Byers, personal communication) and would contribute to a better understanding of why this effect was much stronger in 2000 (decrease of the catches when entering the Sonian forest) compared with 1999 (no reduction of the catches). Further experiments, such as the mark-release-recapture approach, in both

mixed coniferous and broadleaved stands would provide an interesting confirmation of this hypothesis.

In summary, it is believed that most of the variability in presence of the observed population of *I. typographus* in the city of Brussels is a consequence of external fluxes stemming from native populations (from Wallonia), and resulting in a centre–periphery increasing population gradient. The variability in trap catch data thus results from the variability in population levels (centre–periphery gradient) in combination with changes in the efficiency of traps relating to their accessibility (< 4200 m in the more dense urban area), or to disruption of the bark-beetle response (> 4200 m, when there are no longer any problems of trap accessibility but a high proportion of broadleaved trees in the vicinity of the traps).

We caught a much higher number of insects near the port of Brussels than would have been expected from such a highly urbanized location. We made visual observations of galleries and individuals from several bark beetle species on imported timber stocked in the port of Brussels. These logs may have been infested at their location of origin or during transportation; hence, their actual origin could only be established through genetic analysis. However, this observation indicates that, together with the influx of insects from the periphery, the trade of timber over long distances is a potentially important introduction pathway for exotic insects. There is no restriction (barking or controlling) on importing spruce timber from Russia or the Baltic States provided that its area of origin is considered as being included in geographical Europe. In the wider context of an increase in worldwide commercial exchanges and the associated threat of invasive species, it may be crucial to understand how these insects establish in distant urban habitats and to which economic or social activities their movements are related.

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