

Research Article

Declining Bark Beetle Densities (*Ips typographus*, Coleoptera: Scolytinae) from Infested Norway Spruce Stands and Possible Implications for Management

Alexander Angst,¹ Regula Rüegg,² and Beat Forster¹

¹Research Unit Forest Dynamics, Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

²Department of Environmental System Sciences, Swiss Federal Institute of Technology ETH, ETH-Zentrum, 8092 Zürich, Switzerland

Correspondence should be addressed to Beat Forster, beat.forster@wsl.ch

Received 15 September 2011; Revised 22 December 2011; Accepted 28 December 2011

Academic Editor: John A. Byers

Copyright © 2012 Alexander Angst et al. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

The eight-toothed spruce bark beetle (*Ips typographus*) is the most serious insect pest in Central European forests. During the past two decades, extreme meteorological events and subsequent beetle infestations have killed millions of cubic meters of standing spruce trees. Not all the infested stands could be cleared in time, and priorities in management had to be set. Natural or man-made buffer zones of about 500 meters in width are frequently defined to separate differently managed stands in Central Europe. While the buffer zones seem to be effective in most of the cases, their impact has not been studied in detail. Beetle densities were therefore assessed in three case studies using pheromone traps along transects, leading from infested stands into spruce-free buffer zones. The results of the trap catches allow an estimation of the buffer zone influence on densities and the dispersal of *Ips typographus*. Beetle densities were found to decrease rapidly with increasing distance from the infested spruce stands. The trap catches were below high-risk thresholds within a few hundred meters of the infested stands. The decrease in catches was more pronounced in open land and in an urban area than in a broadleaf stand. Designed buffer zones of 500 m width without spruce can therefore very probably help to reduce densities of spreading beetles.

1. Introduction

The eight-toothed or European spruce bark beetle (*Ips typographus* L.) is, from an economic and ecological point of view, one of the most serious forest pests in Europe [1, 2]. It mainly attacks Norway spruce (*Picea abies* (L.) Karst.). Poorly textured, even-aged, pure stands of spruce are particularly vulnerable. Suddenly exposed spruce on the edges of stands are highly attractive to bark beetles. The pest outbreaks, such as after windstorms or droughts, are likely to trigger dieback of host trees on a large scale within several years. This happened for example after the years 1983 and 1984, when heavy thunderstorms swept over the Bavarian National Park, resulting in an abundance of uncleared wind-felled trees. The following bark beetle outbreak spreads rapidly to the surrounding stands due to favourable weather conditions. Managed spruce stands bordering the park were also affected [3]. In wide parts of Central Europe, the infestations in

the years after the storm “Lothar” in 1999 and again after the hot and dry summer of 2003 were similarly impressive. In Switzerland, the spruce bark beetle killed a volume corresponding to 40% of the spruce increment that grew in the period from 1999 to 2005 [4].

The mass attacks posed a great challenge for the forest services and forest owners. Logistic problems were often the reason why conventional control measures could not be organized in time. A certain amount of wind-felled spruces and infestation spots had to remain uncleared. That is why forest owners and the local authorities have to set management priorities according to what functions the forest has and what type of landscape is involved [5]. A considerably high level of *Ips typographus* infestation can often be observed in disturbed and unmanaged spruce stands such as those in protected areas [6], which leads to a greater beetle pressure on neighbouring managed stands. If managed stands border unmanaged ones, the edges of

cleared infestation spots often become reinfested with bark beetles, due to a high beetle pressure from the uncleared spots. A clever choice of natural spruce-free borders like mountains, meadows, villages, lakes, or broadleaf stands help to minimize such buffer-zone problems between managed and unmanaged spruce stands.

Because the distance of *I. typographus*' active dispersal flights is believed to vary within a few hundred meters, a buffer zone of 500 meters between uncleared infested stands and managed forests is recommended in forest practice. If a spruce-free belt cannot be selected, intense monitoring takes place within the buffer zone and beetle attacked trees will be felled and removed or debarked. Within such a zone, no infested spruce is tolerated.

The safety distance of 500 meters is based on the experience of field foresters and the results of several studies. The GIS-based study of Wichmann and Ravn [7] showed that the short distance dispersal of beetles is less than 500 meters since at a distance of more than 500 meters an area with wind-thrown or infested trees has no significant influence on a beetle population. Similar findings were obtained in the Bavarian National Park. Despite heavy infestation pressure, Heurich et al. [3] found that a reinfestation in the peripheral zone could be limited to a distance of 500 meters. Becker and Schröter [8] showed that standing attacks markedly decreased 500 meters away from the primary infestation spot. On the other hand, Duelli et al. [9, 10], who investigated the migrational behaviour of the spruce bark beetle and their flight patterns outside forests or outside spruce stands in situations with a low beetle impact, did not observe such a clear decrease. In contrast to these dispersal studies in areas with a low beetle density, in the present study, we analyzed distance-dependent beetle captures emanating from stands with high beetle densities and infestations on standing spruce. In particular, we wanted to clarify whether the postulated minimal width of a buffer zone of 500 meters is reasonable and if it can be recommended for control strategies in Switzerland. What is relevant in this case is that the impact decreases sufficiently within this distance to reduce the infestation risk for neighbouring stands. So the goal was not to ascertain the origin of all the captured beetles, but rather to find out whether there is a distance-dependent decrease in beetle pressure emanating from known infestation spots.

2. Materials and Methods

2.1. Study Areas. For our study, we focused particularly on forest districts with a high beetle infestation in the previous year, which had resulted in considerable compulsory fellings, infestations spots, and beetle catches in pheromone traps. The research areas were chosen to include Norway spruce stands bordering large open areas or pure broadleaf stands. No experiments within spruce stands were conducted because it would not have been possible to specify how many of the beetles caught in the traps spread from the initial infestation spots without marking and releasing beetles.

All transects started at spots or stands that had been infested by *Ips typographus* in the previous year. In all three

study areas, the *I. typographus* populations were bivoltine as the altitude varies between 400 and 700 m a.s.l. The preliminary transect of 2006 led to a city (Figure 1(a)) and the 2008 transects led to an open area (Figure 1(b)), and a broadleaf stand (Figure 1(c)). The transect in the city of Zurich (8°33'51.56"/47°23'4.35") was approximately 2,000 meters long. It started on the Zurichberg (Figure 1(a)) in a mixed stand with several uncleared infestation spots within a few hundred meters and then went southwest towards the city centre (main station). It crossed an urban area with green spaces and gardens, where some scattered Norway spruce occur as ornamentals.

In Oberbüren (9°10'36.24"/47°26'23.74") in Canton St. Gallen, transect b was nearly 1,000-meter long (Figure 1(b)). It led from west to east with an uphill slope of just 3%, away from a formerly infested Norway spruce forest edge to an open area (9°13'44.1"/47°26'3.06"). The traps were set up along the talus of a motorway several dozen meters away from traffic. The Norway spruce stand had scattered infestations in the previous years on an area of nearly 20 hectares.

The 1,320-meter-long transect c at Renedaa near Reutene (9°2'47.65"/47°39'8.32") in Canton Thurgau (Figure 1(c)) led northwest with a downward slope of 7% into a broadleaf stand (9°2'0.52"/47°39'34.87") of about 45 hectares. This transect started in a recently cleared infestation spot within a mixed stand of roughly 2.5 hectares containing Norway spruce. The transect went through an almost pure broadleaf stand (mainly European beech, *Fagus sylvatica*) with only a few single spruce trees, silver firs (*Abies alba*), and Scots pines (*Pinus sylvestris*), all without any bark beetle infestations. The second half of transect c followed a forest road.

2.2. Arrangement of the Traps. Four to seven pairs of black slit traps were set per transect. The lure in all traps was Pheroprax of BASF, a synthetic aggregation pheromone, based on (S)-*cis*-verbenol and methylbutenol. The traps were arranged pairwise to average out the influences of the microlocations and eventual lure irregularities. The trap arrangement in Zurich was somewhat different from the others. Only four pairs of traps were used. The distance between the single traps within a pair varied in this case between 10 and 90 meters, with the traps often set up on buildings (roofs, terraces) to prevent vandalism.

In the two 2008 experiments, a pair of traps was positioned at each sampling point with the upper end of the trap at breast height (1.3 meter). The trap pairs had a gap of approximately 10 meters between the single traps. The front side of the trap was arranged so as to have as much antemeridian and midday sun as possible. Furthermore, care was taken to place the traps at homogeneous microlocations to ensure catch conditions were as uniform as possible.

The preliminary experiment in Zurich (transect a) was performed in a shortened period from June 19 to August 15, 2006. It did not cover the whole flight activity of the overwintered *Ips typographus* generation. The traps in transects b and c were installed on April 23 and 24, 2008, and immediately baited with the attractants. The traps were last emptied and then removed on September 11, 2008. Exactly

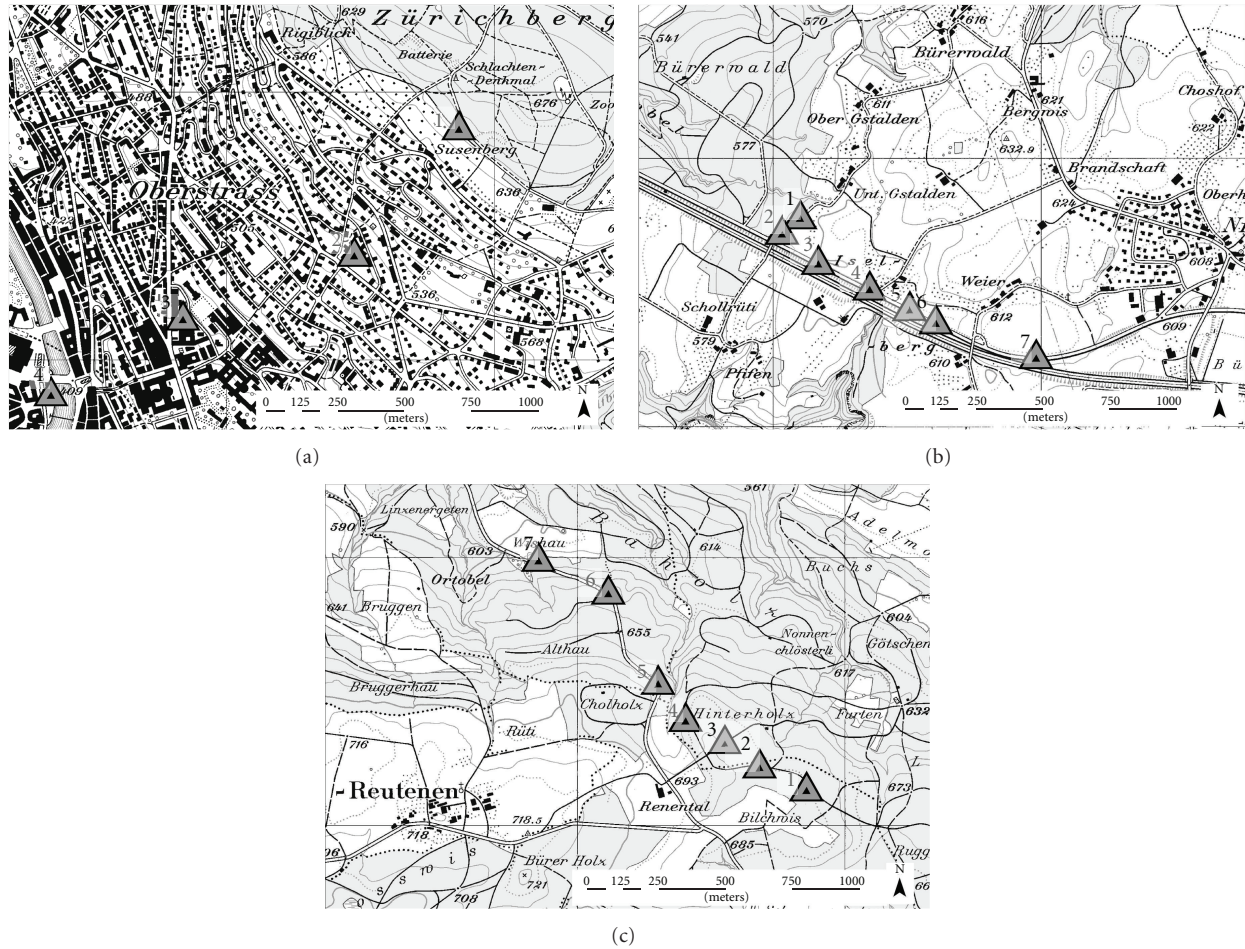


FIGURE 1: The design of the trap transects in (a) the city, (b) the open land, and (c) the broadleaf stand. All transects start in stands with infestations spots. (Maps: VECTOR 25, swisstopo (JA100118), 2010.)

every 14 days, the traps were inspected, emptied, and the beetles counted.

2.3. Data Analysis. The data were plotted with the program DataDesk (Version 6.3, Data Description, Inc., Ithaca, NY), and a curve was fitted to the points. For the “fall-off of density with distance,” the equation of the type $y = a + bx$ was applied, or rather an improvement on it: $y = e(a + bxc)$, according to Southwood [11], where x is the number of beetles and y is distance from the infestations. The curve with the best fit was that of Hawkes [12] of the type $y = e(a + b\sqrt{x})$. Duelli et al. [10] used this formula to represent the spread of freshly emerged beetles. This equation assumes that the lengths of individual moves are not haphazard and random [11]. The coefficient of determination R^2 was calculated to describe the correlation. For the whole analysis, the sample pairs were not pooled. Instead, the single traps within the pairs were used.

3. Results

3.1. Number of Beetles Caught. All pheromone traps caught at least a few specimens of *Ips typographus*, and the catches

decreased with the distance to the infested stands (Figure 2). The average number of the catches per trap and transect ranged between 2,500 beetles in the city (transect a), 3,600 beetles in the open area (transect b), and 11,300 beetles in the broadleaf stand (transect c). Because all transects lead away from former infested stands or spots, it makes more sense to compare the trap catches in or near the infestation area only. This means the catches at the starting points of the transects are higher and demonstrate a considerable infestation level. At the starting point of transect c in the broadleaf stand, the catches (25,300) are about twice as high as at the starting point of transect b in the open area (11,200). The catches at the starting point of the city transect a (9,400) are below this value, but they were caught during a shorter trapping period that excluded the first flight in spring, which is when a high flight density of beetles is usual [13].

3.2. Beetle Densities in the City, Open Land, and Mixed Deciduous Stand. Along all transects, a clear decrease in the numbers of bark beetles individuals was monitored (Figure 2). In the city of Zurich, along transect a, the calculated curve of the catches declines quickly: after 40 meters, the beetle density was only half that in the forest and after 680 meters

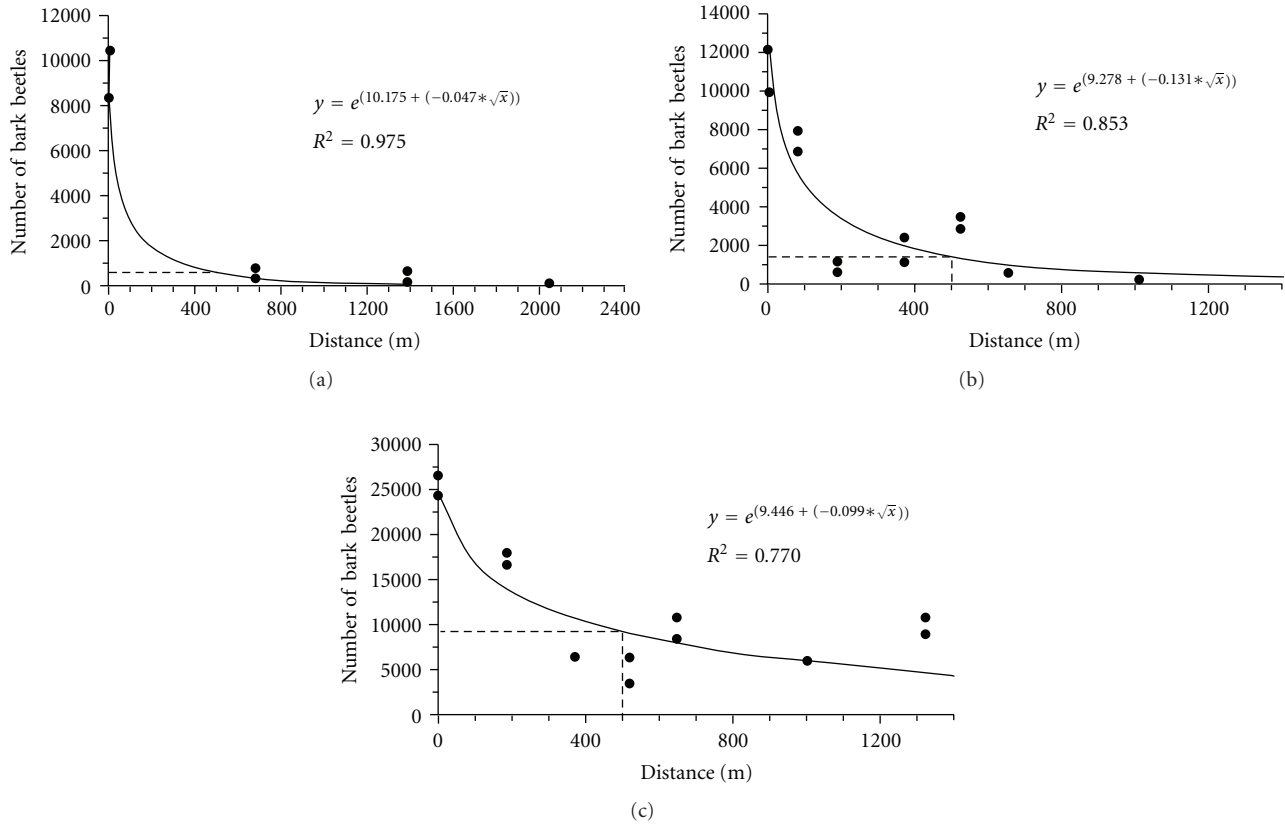


FIGURE 2: Trap catches of *Ips typographus* in the city (a), in the open land (b), and in the broadleaf stand (c), starting from infested spruce. The calculated beetle density 500 meters from the infestation spot is marked.

only 4%. At a distance of 500 meters, it was calculated that 572 beetles would have been caught per trap, that is, only about 7% of the initial trap catches in the forest (Figure 2(a) and Table 1). In this preliminary study in 2006, the fast decrease in beetle density was possibly a consequence of having no traps between the infested stand with the first trap pair and the second trap pair already 680 meters away. Therefore, a goal of the other two case studies from 2008 was to fill in these gaps by including results from traps set closer to the infested stands.

The numbers of catches in the open area (transect b) declined also rather fast. The density dropped after just 200 meters to only one-fourth (Figure 2(b)). A second tiny peak at about 500 meters distance from the infestation point was probably due to a small and isolated spruce group bordering the open area to the south. This could have been a source of irregularity, which resulted in an increased number of catches at this trapping point. According to the applied regression formula by Hawkes [12], we estimated that 1,383 beetles would have been caught at a distance of 500 meters.

After the first 400 meters, the catches in the broadleaf stand (transect c) reached only one-fifth of the number of catches of the first trap pair. But at a distance of 500 meters, we calculated there would have been still 9,173 beetles. Towards the end of the transect, the catches even out to a level of about 7,500 beetles (Figure 2(c)). It can be assumed that this reflects the basic flight density level in this 45 hectare

TABLE 1: Calculated values for the catches (beetles per trap) in (a) the city, (b) the open land, and (c) in the broadleaf stand transect.

	(a) City	(b) Open land	(c) Broadleaf stand
Catches at 500 m (n)	572	1,383	9,173
Catches at 500 m (%)	7%	12%	36%
50% catches at	40 m	70 m	250 m
5% catches at	570 m	990 m	4,160 m

broadleaf stand that bordered forests with infested spruce. The population density seems to have been much higher in the broadleaf stand (c) than in the open area (b).

The differences between the trap catches in the three investigation areas are shown in Figure 2. Whereas the number of beetles caught per trap in the broadleaf stand was more than twice that in the open land and in the city, the “broadleaf” curve does not decrease as fast as the other two. The beetle density in the deciduous stand was at least twice as high as in the open land or the city.

In the open area, a marked decline was observed after just 200 meters. The basic population evened out to a low level of about 1,000 beetles per trap. In the broadleaf stand, the gradient also declined rapidly but evened out to a considerable level of 7,500 beetles per trap. The population density halved at approximately 250 meters, much further than in the open land or in the city. At a distance of

500 meters, the catches still added up to 36% that at the beginning of the transect.

4. Discussion

4.1. Beetle Pressure and Frequency of *Ips typographus*. Altogether, a minimum of 61 beetles per trap were caught over the whole period in the city and a maximum of 26,405 beetles per trap at the beginning of the broadleaf stand transect. These figures indicate that *I. typographus* was present in all the studied areas and support the conclusion of Piel et al. [14], who claimed that this species is able to spread over large areas, even though the host tree is relatively rare. According to Duelli et al. [9], who studied the beetle flight in a low impact situation, considerably more beetles can be found in the forest than outside. Sanders [15] used pheromone traps to demonstrate that bark beetles pass through broadleaf forests in their dispersal flight during the latent phase. Gugerli et al. [16] found that the basic beetle population, and consequently also the mass reproduction, does not differ much genetically in space. This may indicate that there is a constant and significant gene exchange by migrating beetles.

It should be remembered that trap catches do not necessarily represent the actual population density, flight activity, and the migration of the spruce bark beetle, as described by Zolubas and Byers [17]. Zúmr [18] and Duelli et al. [10] performed recapture experiments and found that, besides the released beetles, many other feral individuals were trapped. It is always difficult to interpret trap catches without considering the attractiveness of the host trees and the potential breeding material. Nevertheless, the above experiments and the present research show that the spread and area-wide distribution of *Ips typographus* are impressive. It would be possible to build up new mass attacks nearly anywhere in the forest if suitable breeding material is present and the weather conditions are favourable.

Under our study conditions, however, the population quickly thinned within 300 to 400 meters of an infestation spot (Figure 2), particularly outside the forest. Since beetles have very little chance of breeding in the conditions along the chosen transects, the numbers of beetles caught along the transects reflect the impact of the beetle populations rather well.

It was striking that three times more beetles were caught in the broadleaf stand than in the open area. There are several possible reasons for the relatively high number of catches in the deciduous forest. First, beetles probably prefer to swarm in forests. As already mentioned, Duelli et al. [9] found considerably more beetles in the forest than outside. In Norway, Botterweg [19] observed that *I. typographus* spreads homogeneously throughout forested areas. Second, we were not able to find an absolutely pure deciduous forest with an isolated infected spruce stand nearby. Hence, the stand with a very few sporadically scattered spruce trees had to be accepted for the experiment, and these could have influenced the number of catches slightly, even though the trees were in good sanitary condition. Healthy spruce trees are not in strong competition with pheromone traps, and it can be assumed that the traps in our study were highly attractive and thus

reflected the spreading behaviour of *I. typographus*. On the open land transect, a small strip of woodland may have interfered with the traps at 512 m distance. The small stand, which lies south of the traps across the motorway, contains some Norway spruce. It cannot be excluded that some of the bark beetles caught originated or were influenced by this stand.

The results from study-site a in the city should, however, be treated with caution, as the second trap pair was 680 meters away from the infestation spot and no data were collected between the first and the second trap pair.

The research areas were chosen to include infested Norway spruce stands that bordered directly onto an adequate open or urban area and onto a preferably pure broadleaf stand. We consciously did not choose transects within spruce stands because, without releasing marked beetles, it would not have been possible to identify the proportion of the trap captures that did not originate from the initial infestation spots. To simulate high beetle pressure artificially, several hundred thousand marked beetles would be necessary, which would pose an impractical logistical challenge. It is not, in fact, clear that all individuals caught in the traps have a common origin. Nevertheless, on all transects, the population thinned quickly within only a few hundred meters, regardless of the origin of the beetles.

4.2. Buffer Zones. Up to now, forest managers have tended to use an empirically derived rule that specifies that a combat and/or buffer zone of 500 meters around an infested stand prevents a substantial invasion into the adjacent forests [20–22]. Byers [13] maintained that a border area of 500 meters width is justifiable under epidemic conditions. This rule has often been applied in Central Europe but until now has never actually been tested experimentally. On the basis of a GIS analysis, Wichmann and Ravn [7] concluded that epidemical attacks only spread out across short distances of less than 500 meters. The present study of high beetle impact indicates that a clear decline in the beetle population takes place within the first 300 meters away from the infestation spot. It then evens out to a level that does not pose an imminent danger to surrounding Norway spruce stands. If the buffer zone is an open area, the population may even decline considerably within the first 200 meters. The findings of our study indicate therefore that open areas may provide very suitable border zones between managed and unmanaged stands and help lower high beetle pressure from a control-free infested stand.

Infestations of living spruce trees are likely to occur in Switzerland when there are over 12,000 beetles caught per pheromone trap and year as mentioned by Forster and Meier [23]. Above this threshold, there is a considerable risk that the spruce bark beetle will locally spread and attack new trees. Various authors have reported similar thresholds: in Swedish spruce forests between 10,000 [24] and 15,000 [25] beetles per trap and year and between 8,000 [26] and 10,000 [27] beetles per trap and year in Northern Italy. Thus, the estimate of 12,000 beetles for Swiss spruce forests seems reasonable. In most of the cases, the beetles spreading from infestation spots will very likely thin out within the first 300 meters without spruce and densities will drop under the above threshold. This means that a buffer zone 500 meters in

width [13] is probably on the safe side. This study therefore confirms the hypothesis that the bark beetle density declines considerably within the first 500 meters of a spruce free buffer zone (Table 1). For all these reasons, such a buffer zone can be recommended.

Whether such buffer zones inhibit a further enlargement of beetle-infested stands should be always considered critically. If the host tree resistance is low, new trees will be successfully colonized by a smaller quantity of migrating beetles. However, it seems possible to considerably reduce the spread of bark beetles through implementing forest protection strategies and well-timed and consistent control measures, at least where conditions are similar to those at the sites we studied.

However, some beetles can be transported by wind much further, even though there are usually no active and directed immigration flights over long distances. The population in such cases thins out quickly, and a new breeding locality is chosen more or less random. To spread geographically, the beetles have to build up first a new population at a distant infestation spot.

4.3. Consequences for Bark Beetle Management. The findings of this study should be used in bark beetle management practices, especially under difficult conditions where there is a need for buffer zones between managed and unmanaged spruce stands. What is crucial is that management priorities should be defined on a large enough scale on the basis of well-defined landscape compartments. Compartments for the interventions should be chosen to be at least 100 hectares in size. At the same time, natural area borders (mountains, meadows, villages, lakes) 500 meters in width will also help to improve the effectiveness of selected buffer zones [28]. Setting such spatial priorities in bark beetle management and clearly defining and separating areas can reduce the spread of beetle infestations and infestation pressure.

The present study does not refer to buffer zones between managed and unmanaged, differently infested spruce stands that directly border each other. Experience has shown that under such conditions, stand edges of cleared spots within selected buffer zones are often reinfested. In the worst case, infestations may continue until all spruce trees in the zone have been attacked and subsequently removed. Under such high-risk conditions, the flight behaviour and beetle pressure of *Ips typographus* may be different. This still needs to be studied in detail.

Acknowledgments

The authors are grateful to Professor Dr. Peter Duelli, Dr. Andreas Rigling and Dr. Beat Wermelinger for their helpful suggestions for improving the paper. They also thank the forest services of the Cantons Thurgau, St. Gallen and Zurich, especially their forest protection agents and field foresters, for their cooperation, Thomas Reich for lending a helping hand setting up the traps, Franz Meier for valuable discussions, and Dr. Silvia Dingwall for her linguistic corrections. This

study received financial support from the Federal Office for the Environment (FOEN) in Berne.

References

- [1] F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire, and H. F. Evans, *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis*, Kluwer Academic Publishers, Dordrecht, The Netherlands, 2004.
- [2] B. Wermelinger, "Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research," *Forest Ecology and Management*, vol. 202, no. 1–3, pp. 67–82, 2004.
- [3] M. Heurich, A. Reinelt, and L. Fahse, "Die Buchdruckermassenvermehrung im Nationalpark Bayerischer Wald," in *Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall*, M. Heurich, Ed., vol. 14 of *Bayer. Staatsforstverwaltung, Wiss. Reihe*, pp. 9–48, Grafenau, Germany, 2001.
- [4] B. Forster, F. Meier, and U. B. Brändli, "Deutlicher Rückgang der Fichte im Mittelland—Vorratsabbau auch durch Sturm und Käfer," *Wald Holz*, vol. 89, no. 3, pp. 52–54, 2008.
- [5] B. Forster, F. Meier, R. Gall, and C. Zahn, "Erfahrungen im Umgang mit Buchdrucker-Massenvermehrungen (*Ips typographus* L.) nach Sturmereignissen in der Schweiz," *Schweizerische Zeitschrift für Forstwesen*, vol. 154, no. 11, pp. 431–436, 2003.
- [6] H. Schröter, "Ausbreitung des Borkenkäferbefalls in Bannwäldern Baden-Württembergs," in *Forstschutzprobleme in Nationalparks und Naturschutzgebieten*, A. Wulf and K. H. Berendes, Eds., vol. 362 of *Mitteilungen Biologische Bundesanstalt Land-Forstwirtschaft*, pp. 63–79, Berlin, Germany, 1999.
- [7] L. Wichmann and H. P. Ravn, "The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS," *Forest Ecology and Management*, vol. 148, no. 1–3, pp. 31–39, 2001.
- [8] T. Becker and H. Schröter, "Ausbreitung von rindenbrütenden Borkenkäfern nach Sturmschäden," *Allgemeine Forstzeitung*, vol. 55, no. 6, pp. 280–282, 2000.
- [9] P. Duelli, M. Studer, and W. Näf, "Der Borkenkäferflug ausserhalb des Waldes," *Zeitschrift für Angewandte Entomologie*, vol. 102, pp. 139–148, 1986.
- [10] P. Duelli, P. Zahradnik, M. Knizek, and B. Kalinova, "Migration in spruce bark beetles (*Ips typographus* L.) and the efficiency of pheromone traps," *Journal of Applied Entomology*, vol. 121, no. 1–5, pp. 297–303, 1997.
- [11] T. R. E. Southwood, *Ecological Methods with Particular Reference to the Study of Insect Populations*, Chapman & Hall, London, UK, 1978.
- [12] C. Hawkes, "The estimation of the dispersal rate of the adult cabbage root fly (*Erioischia brassicae* (Bouché)) in the presence of a brassica crop," *Journal of Applied Entomology*, vol. 9, no. 2, pp. 617–632, 1972.
- [13] J. A. Byers, "Wind-aided dispersal of simulated bark beetles flying through forests," *Ecological Modelling*, vol. 125, no. 2–3, pp. 231–243, 2000.
- [14] F. Piel, M. Gilbert, A. Franklin, and J. C. Grégoire, "Occurrence of *Ips typographus* (Col., Scolytidae) along an urbanization gradient in Brussels, Belgium," *Agricultural and Forest Entomology*, vol. 7, no. 2, pp. 161–167, 2005.
- [15] W. Sanders, "A contribution to the behaviour of the Scolytid *Ips typographus* L. during the flight period," *Anzeiger für Schädlingskunde Pflanzenschutz Umweltschutz*, vol. 57, no. 7, pp. 131–134, 1984.

- [16] F. Gugerli, R. Gall, F. Meier, and B. Wermelinger, "Pronounced fluctuations of spruce bark beetle (Scolytinae: *Ips typographus*) populations do not invoke genetic differentiation," *Forest Ecology and Management*, vol. 256, no. 3, pp. 405–409, 2008.
- [17] P. Zolubas and J. A. Byers, "Recapture of dispersing bark beetle *Ips typographus* L. (Col., Scolytidae) in pheromone-baited traps: regression models," *Journal of Applied Entomology*, vol. 119, no. 2, pp. 285–289, 1995.
- [18] V. Zurr, "Dispersal of the spruce beetle *Ips typographus* (L.) (Col., Scolytidae) in spruce woods," *Forest Ecology Management*, vol. 114, no. 1–5, pp. 348–352, 1992.
- [19] P. F. Botterweg, "Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content," *Zeitschrift für Angewandte Entomologie*, vol. 94, no. 1–5, pp. 466–489, 1982.
- [20] H. Schröter, "Borkenkäferproblematik im Nationalpark Bayerischer Wald," in *Borkenkäferproblematik im Nationalpark Bayerischer Wald*, C. Wild, J. Metzger, and C. Strauss, Eds., pp. 16–19, Bayerische Landesanstalt für Wald und Forstwirtschaft, Freising Germany, 1998.
- [21] Nationalparkverwaltung Berchtesgaden, *Nationalparkplan*, Bayer. Staatsministerium für Landesentwicklung und Umweltfragen, München, Germany, 2001.
- [22] G. Lobinger, "Rindenbrütende Borkenkäfer an Fichte," *LWF Merkblatt*, vol. 14, p. 6, 2004.
- [23] B. Forster and F. Meier, "Die Borkenkäfersituation 1989/90, Buchdrucker (*Ips typographus*)," *PBMD-Bulletin*, vol. 7, p. 18, 1990.
- [24] J. Weslien, "Monitoring *Ips typographus* (L.) populations and forecasting damage," *Journal of Applied Entomology*, vol. 114, no. 1–5, pp. 338–340, 1992.
- [25] Å. Lindelöw and M. Schroeder, "Spruce bark beetle, *Ips typographus* (L.), in Sweden: monitoring and risk assessment," *Journal of Forest Science*, vol. 47, pp. 40–42, 2001.
- [26] M. Faccoli and F. Stergulc, "A practical method for predicting the short-time trend of bivoltine populations of *Ips typographus* (L.) (Col., Scolytidae)," *Journal of Applied Entomology*, vol. 130, no. 1, pp. 61–66, 2006.
- [27] P. Ambrosi, D. Angheben, and C. Salvadori, "Tecniche di difesa e di controllo delle popolazioni di scolitidi in boschi di conifere," *Monti e Boschi*, vol. 3, pp. 22–26, 1990.
- [28] B. Forster and F. Meier, "Sturm, Witterung und Borkenkäfer. Risikomanagement im Forstschutz," *Merkblatt für die Praxis*, vol. 44, p. 8, 2008.

