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The arthropod complex associated with *Ips typographus* (L.) (Coleoptera, Scolytidae): species composition, phenology, and impact on bark beetle productivity

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The biology of forest arthropods associated with the bark beetle *Ips typographus* and the impact of these associates on bark beetle productivity were investigated in the field. Arthropods were allowed access to spruce bolts for different lengths of time, 0, 1, 4, and 8 weeks, following onset of attack by *Ips typographus*, after which time the bolts were moved to a nonforested area and caged. Arthropods were collected as they emerged from the bolts in autumn and the following spring. At least 32 arthropod species were collected, of which 17 are known to feed on bark beetle brood. The longer the exposure period the more bark beetle enemies and the fewer *Ips typographus* emerged. Natural enemies were estimated to have reduced bark beetle productivity by 83%. Arrival and emergence patterns and relative impact on bark beetle productivity of different species are discussed.

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1. Introduction

Most species of bark beetles (Scolytidae) breed under the bark of woody plants. The bark offers protection from many generalist predators, but a great number of predators and parasites are specialists that can attack the subcortical life stages (see e.g. Dahlsten 1981, Mills 1983, Moeck & Safranyik 1984).

Field studies have shown that natural enemies can reduce bark beetle emergence significantly (Moore 1972, Linit & Stephen 1983, Miller 1984, 1986, Riley & Goyer 1986). All of these studies were made in the southeastern part of North America. This region has a warm climate, and the bark beetles have several generations per year, which may favour the build-up of predator and parasite populations. Few quantative studies on the impact of natural enemies on bark beetle productivity have been done in temperate regions with univoltine bark beetles (see Scandinavian studies referred to below).

The spruce bark beetle *Ips typographus* (L.) is one of the most injurious insects attacking Norway spruce, *Picea abies* L. (Karsten) in Eurasia. The biology of this bark beetle has been intensively studied, and the arthropod complex associated with it is well known. About 140 arthropod species mainly from the orders Coleoptera, Diptera, Hymenoptera, and Acarida, have been documented to occur in *Ips typographus* galleries in Europe. Many of these species are saprophagous or have unclear feeding habits but at least 60 of them have been reported to feed on the immature stages of bark beetles (Saalas 1917, Sachtleben 1952, Hedqvist 1963, Nuorteva 1956, 1957, 1958, Klausnitzer & Förster 1974, Merlin et al. 1986, Moser & Bogenschütz 1984, Moser et al. 1989, Õunap 1980, 1986).

Field experiments in Scandinavia indicated that mechanical exclusion of natural enemies from stems attacked attacked by *Ips typographus* led to an increase in bark beetle productivity (Pettersen & Tvermyr 1971, Weslien & Regnander 1992). However, in these studies the exclusion was not total, and all insects involved were not thoroughly counted and determined to species.

The phenology of many insect species associated with *Ips typographus* in Fennoscandia is not well known. This is true for the time of arrival at attacked trees as well as for the time for emergence from these trees.

The aim of the present study was to estimate the impact of predation and parasitism under bark on the productivity of *Ips typographus*. It was of high priority to determine the density and the arrival and emergence times of the different species involved.

2. Materials and methods

The study site was located 15 km north of Uppsala in central Sweden. Along a forest edge bordering a 5-year-old clear-felling, spruce bark beetle attacks had occurred on windthrown and standing spruce trees for at least three years prior to the study (1983–1985). It was therefore assumed that a build-up of natural enemy populations had occurred in the area. Bark samples taken in November 1985 confirmed that larvae of Diptera and Hymenoptera were abundant. In 1985 two standing trees and four fallen trees had been colonized by *Ips typographus*.

In early spring 1986, two spruce trees were felled, and 12 bolts (length 65–70 cm, diameter 16–22 cm, mean bark area 0.35 m^2) were cut from each tree. The ends of the bolts were sealed with paraffin to prevent severe desiccation.

The experiment had a randomized block design with six blocks and four treatments. Each block consisted of four neighbouring bolts (i.e. a stem section cut in four pieces). Insects were allowed access to the bolts for different lengths of time following attack by *Ips typographus*. The treatments were:

0W = no exposure; bark beetles were released on the bolts in cages.
1W = exposure for 1 week after the first observed *Ips typographus* attacks.
4W = exposure for 4 weeks after the first observed *Ips typographus* attacks.
8W = exposure for 8 weeks after the first observed *Ips typographus* attacks.

Exposure was discontinued by putting the bolts in screen cages (83 × 44 × 44 cm, 1 mm screening), that were held in a nonforested area (in Uppsala). The bolts were moved to this area with low populations of forest insects, since small parasitoids and predators might otherwise have entered through the screen.

Bolts in the 0W treatment were stored in Uppsala throughout the experiment. Spruce bark beetles were captured in pheromone traps about 2 km from the experimental site, and 300–400 specimens were released in each cage on 6 June. Thereafter the 0W bolts were held in a greenhouse for 10 days after which time they were moved outside to a shaded place where caged bolts from the other treatments also were held.

The 1W, 4W, and 8W bolts were arranged in blocks in the forest, 30–50 m from the clear-felled area, with ca 10 m between blocks and 10 cm between bolts. All bolts were placed on lying wooden poles to avoid ground contact. On the first day of the flight period, on 20 May, *Ips typographus* attacks were induced with a pheromone bait hung just above each block. As the first attacks were observed, the baits were removed.

On 16 July, each bolt was hung in an emergence trap situated outdoors and in the shade. The trap consisted of a white cotton bag (diameter 40 cm, length 110 cm) with a collecting funnel forming the bottom. Emerging insects were collected 1–2 times weekly from 21 July to 3 Nov. During winter the bolts lay unprotected on the ground. On April 10, the bolts were taken inside and put in paper cartons. Insects emerging in glass vials were collected twice weekly from 14 April to 25 May.

All insects that emerged as adults were determined to species, except Diptera from the genera *Medetera* spp. and *Lonchaea* spp. which were sampled to determine dominant species. Larvae were determined to species if possible, otherwise to genus or family (larvae of many species are not described). Mites (Acarida) were not counted or determined. Once emergence had been completed in May the bolts were stored at –5°C until autumn when the bark on each bolt was peeled off and *Ips typographus* galleries were counted.

3. Results

The longer the bolts were exposed the lower was the productivity of *Ips typographus* (Table 1). This ranking was consistant in each of the 6 blocks. In a two-way analysis of variance, almost all of the variance in productivity was attributable to treatment effects (treatment: $F = 66.5$, $df = 3, 15$, $P < 0.001$; block: $F = 3.8$, $df = 5, 15$, $P < 0.05$).

Breeding density of *Ips typographus* was somewhat higher in the 1W treatment than in the other treatments (Table 1). Much of the variance in breeding density was attributable to block effects (treatment: $F = 7.2$, $df = 3, 15$, $P < 0.01$; block: $F = 19.1$, $df = 5, 15$, $P < 0.001$.

The arthropods that emerged from the bolts are given by number and species (or genus) in Table 2. The later the bolts were caged, the more species were recorded. The total number of arthropods emerging was similar for all treatments, i.e. between 6000 and 6500. Of the total number of emerging artropods, *Ips typographus* comprised 99% in the 0W treatment, 87% in the 1W treatment, 44% in the 4W treatment, and only 19% in the 8W treatment. The corresponding figures for predators and parasitoids were 0.2%, 0.2%, 6.6%, and 21.5% respectively.

Parasitic Hymenoptera were found in all treatments but were abundant only in the 8W treatment. *Lonchaea* spp. and *Quedius plagiatus* occurred exclusively in the 8W treatment. *Thanasimus* spp. occurred in similar numbers in the 4W and 8W treatments as did *Medetera* spp. Small staphylinid larve, mostly *Phloeonomus* spp. were abundant in the 4W and 8W treatments. In contrast to other insect groups, larvae of *Epuraea* spp. were most abundant in the 1W treatment.

In Table 3 emerging arthropods have been pooled in groups according to their size and feeding habits, and the mean number emerging per unit of bark surface is given by treatment and group. The variance in number of emerged specimens for most groups was moderate, and the pattern of occurrence consistant in all blocks (*P. chalcographus*, however, was present only in three blocks).

Diptera were sampled throughout their emergence period. Of 67 sampled specimens of *Medetera* spp., 64 were *M. signaticornis*, 2 were *M. excellens*, and 1 was *M. breviseta*. Of 15 *Lonchaea* spp. all were *L. bruggeri*.

Emergence patterns of different species and genera reveal differences in phenology and overwintering behaviour (Fig. 1). Less than 10% of the *Ips typographus* overwintered under the bark and emerged in spring. In contrast most Diptera overwintered under the bark (*Medetera* spp. 85%, *Lonchaea* spp. 97%). Most of the parasitic Hymenoptera emerged in July and August, but 40% of the *Roptrocerus xylophagorum* emerged the following spring. Most predacious and saprophagous Coleoptera emerged in autumn as larvae.

Median emergence for *Ips typographus* occurred more than one month earlier in the 0W treatment than in the other treatments, indicating that the development rate was faster in that treat-

Table 1. Mean (±*SD*) productivity and breeding density of *Ips typographus* in spruce bolts left uncaged in the forest for 0, 1, 4, and 8 weeks (0W, 1W, 4W, 8W) after the initial attacks of *Ips typographus*. Means followed by different letters are different at 5% probability level (two-way analysis of variance followed by Tukey test).

	0W	1W	4W	8W
Productivity (offspring/egg gallery)	$6.7^{a} \pm 1.2$	$5.3^{b} \pm 0.8$	$2.9^{c} \pm 1.2$	$1.1^{d} \pm 0.4$
Breeding density (egg galleries/m^2)	$420^{a} \pm 55$	$496^{b} \pm 78$	$439^{a} \pm 66$	$451^{ab} \pm 59$

Table 2. Arthropods emerging from spruce bolts left uncaged in the forest for 0 to 8 weeks (0W, 1W, 4W, 8W) after the initial attacks of *Ips typographus*. Total number for 6 bolts per treatment. Feeding habits have been extracted from literature cited in paragraph 3 of Introduction. Abbreviations: L = larva, A = adult, Do = dominant species, Pr= present species, parasitoid L, P, or A = parasitoid of bark beetle larvae, pupae or adult respectively. * = found when peeling bolts, ** = at least two species.

	Stage	0W	1W	4W	8W	Feeding habit
Insecta						
Coleoptera						
Staphylinidae						
Quedius plagiatus (Gyllenhal)	A	0	0	0	5	predator
	L	0	0	0	15	predator
Nudobius lentus Erichsson	A	0	0	0	2	predator
	L	0	0	0	4	predator
Phloeonomus sjoebergi Strand	A	1	5	4	18	unclear
Phloeonomus spp.	L	14	27	148	290	unclear
Leptusa pulchella (Mannerheim)	A	0	0	0	2	unclear
Phloeopora testacea Mannerheim	A	0	0	1	5	unclear
Placusa incompleta Sjöberg	A	0	0	0	4	unclear
Staphylinidae, unknown genus	L	0	1	63	108	unclear
Histeridae						
Plegaderus vulneratus (Panzer)	A	0	0	0	1	predator
Plegaderus spp.	L	0	0	0	2	predator
Cleridae						
Thanasimus spp	L	0	0	23	25	predator
Nitidulidae						
Epuraea thoracica Tournier	A	1	0	0	1	unclear
E. pygmaea (Gyllenhal)	A	0	0	2	1	unclear
Epuraea spp.	L	26	786	39	99	unclear
Rhizophagidae						
Rhizophagus dispar (Paykull)	A	0	0	0	2	scavenger
	L	0	0	0	9	scavenger
R. ferrugineus (Paykull)	A	0	1	0	10	predator
Cerambycidae						
Rhagium inquisitor (L.)*	L	0	0	0	39	phloem-feeding
Scolytidae						
Ips typographus (L.)	A	6422	5640	2846	1129	phloem-feeding
Pityogenes chalcographus (L.)	A	2	6	475	313	phloem-feeding
Dryocoetes autographus (L.)	A	0	0	10	63	phloem-feeding
Crypturgus spp.**	A	0	0	2205	2481	phloem-feeding
Hymenoptera						
Pteromalidae						
Roptrocerus brevicornis Thomson	A	0	0	14	90	parasitoid L P
R. xylophagorum Ratzeburg	A	0	2	35	280	parasitoid L P
Rhopalicus tutele Walker	A	0	1	2	466	parasitoid L P
Dinotiscus eupterus Walker	A	0	0	0	23	parasitoid L P
Tomicobia seitneri Ruschka	A	13	3	6	6	parasitoid A
Karpinskiella pityophtori Boucek	A	0	1	3	4	parasitoid A
Braconidae						
Rhopalophorus clavicornis Wesmael	A	0	0	0	3	parasitoid A
Cosmophorus regius Nietzabitowski	A	0	0	0	1	parasitoid A
Diptera						
Dolichopodidae						
Medetera signaticornis Loew	A	0	1	Do	Do	predator
M. excellens Frey	A	0	0	Pr	Pr	predator
M. breviseta Parent	A	0	0	Pr	Pr	predator
Medetera spp. (total)	A	0	1	331	356	predator
Lonchaeidae						
Lonchaea bruggeri Morge	A	0	0	0	Do	unclear
Lonchaea spp. (total)	A	0	0	0	132	unclear
Stratiomyidae						
Zabrachia minutissima Zetterstedt	A	0	0	0	10	scavenger
Arachnoidea						
Pseudoscorpionida						
Chernes cimicoides (F.)	A	0	0	0	2	predator
	L	0	0	0	6	predator
Total artropodods (excl. Acarida)		6479	6474	6207	6007	
Total species (minimum)		5	11	18	32	

ment, probably due to higher temperature during storage in the greenhouse. The emergence patterns of *Ips typographus* were similar for the 1W, 4W, and 8W treatments (median emergence date 13–17 September).

4. Discussion

The exclusion of insect associates led to a 6-fold increase in *Ips typographus* productivity (Table 1, 0W vs 8W). In other words, the natural enemies reduced bark beetle productivity by 83%. The same relative difference was reached in bark beetle emergence (Table 3). This difference, as well as the density of predators and parasitoids are in agreement with the results of Linit & Stephen (1983) for *Dendroctonus frontalis* Zimmerman (82% reduction, 366 predators and 336 parasitoids per m^2, cf Table 3) In other studies with similar densities of predators in the exposure treatment, but with virtually no parasitoids, the differences between exclusion and exposure treatments was 30-40% (Miller 1986, Riley & Goyer 1986).

Obviously natural enemies was the main cause for the large differences in bark beetle productivity between treatments. Other factors that could have affected differences in productivity are the higher breeding density in the 1W treatment and the faster development in the 0W treatment. It is unclear what effect, if any, developmental rate had on productivity in this case. There is an inverse relationship between breeding density and productivity (see e.g. Thalenhorst 1958). Productivity drops as breeding density increases and levels off at high densities. In this study productivity should not have been too sensitive to variations in breeding density since density was high in all bolts.

The difference in productivity between the 0W and 1W treatments was rather small but consistant in all blocks. Besides differences in developmental rate and breeding density (see above), there was a large difference in the number of emerging *Epuraea* larvae between these two treatments (see Tables 2 and 3). Field observations by Nuorteva (1956) indicate that adults of *E. pygmaea* can feed on *Ips typographus* eggs. The feeding habits of *Epuraea* larvae are not clear.

Table 3. Number of insects emerging per m^2 of bark surface from spruce bolts left ungaged in the forest for 0 to 8 weeks (0W, 1W, 4W, 8W) after the initial attacks of *Ips typographus*. Means of 6 replicates ±95% confidence intervals.

Group of insects	0W	1W	4W	8W
Ips typographus	3072±461	2868±450	1402±560	543±229
Large predators (>10 mm)				
(*Thanasimus, Quedius, Nudobius*)	0	0	11±9	23±11
Small predators				
Medetera	0	0	155±56	166±52
Rhizophagus, Plegaderus, Chernes	0	0	0	8±8
Unclear feeding habits				
small Staphylinidae	7±8	14±8	104±65	198±112
Epuraea	13±21	412±237	20±15	46±24
Lonchaea	0	0	0	64±29
Parasitoids of *Ips*	6±9	3±3	28±35	445±130
Competitors to *Ips*				
Rhagium	0	0	0	19±10
Dryocoetes	0	0	2±5	32±19
Pityogenes	1±3	3±7	241±474	174±265

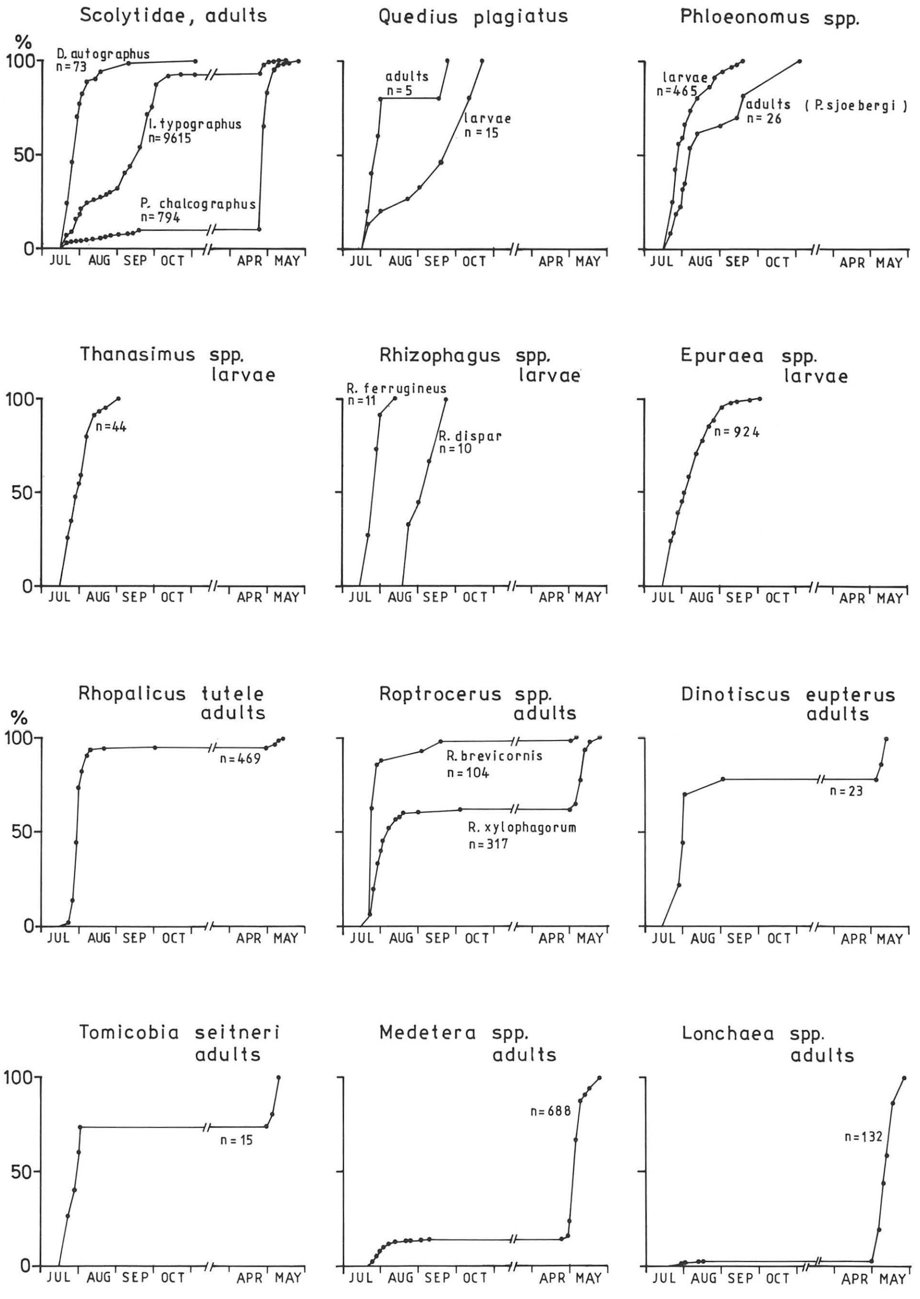

Fig. 1. Emergence patterns of insects emerging from spruce bolts attacked in the forest by *Ips typographus* mainly on 20 and 21 May 1986 (1W, 4W, and 8W treatments).

Observations by Hanson (1937) and Nuorteva (1956) indicate that they can feed on bark beetle brood, whereas Mamaev et al. (1977) considers them not to be entomophagous.

The difference in productivity between 1W and 4W treatments was obviously caused by predators. The predators involved were *Medetera* spp. and *Thanasimus* spp., of which *M. signaticornis* occurred at high densities and was most important.

The large difference in productivity between 4W and 8W treatments can be attributed mainly to the activity of parasitic Hymenoptera, of which *Rhopalicus tutele* and *Roptrocerus xylophagorum* were most abundant. Predation by *Lonchaea bruggeri* and *Quedius plagiatus* as well as other occasional predators, e.g. *Plegaderus vulneratus*, *Chernes cimicoides* and possibly also small Staphylinidae (see below) could have contributed to the observed difference between these treatments.

The fact that the density of *Epuraea* larvae in the 4W and 8W treatments was lower than in the 1W treatment might be explained by treatment-related differences in predator numbers (see Table 3). *Epuraea* larvae were probably eaten by predators.

Larvae of small Staphylinidae e.g. *Phloeonomus* spp. were abundant in the 4W and 8W treatments. Most of the unidentified staphylinid larvae (see Table 2) were probably *Placusa* spp. and *Phloeopora* spp., but I was unable to identify them with certainty. The feeding habits of these small larvae are unclear. They seem to be too small to attack large *Ips typographus* larvae, and in this study most of them arrived too late to attack eggs. Gut content analysis indicated that larvae of *Placusa despecta* Erichson were mycetophagous (Ashe 1990). Field observations indicate that adults of *Phloeopora testacea* (Klausnitzer & Förster 1974, Nuorteva 1956), *Phloeonomus pusillus* Gravenhorst (Langor 1991), and *Placusa tachyporoides* Waltl (= *P. infima*, Escherich 1923:49, citing Fleischer) can eat bark beetle eggs or larvae.

Rhizophagus larvae occurred in low numbers. Of the two species emerging, *R. ferrugineus* and *R. dispar*, the latter seems to be mainly saprophagous (Merlin et al. 1986). There was a clear difference in emergence patterns between the two species (Fig. 1). The emergence patterns of some species e.g. *R. ferrugineus, Epuraea* spp., *Thanasimus* spp., and *Tomicobia seitneri* show that emergence was intensive directly after the bolts were hung in the emergence bags. This indicates that emergence had started before this date. Thus the density of these species might have been underestimated.

Crypturgus spp. (at least two species) occurred in rather high numbers in the 4W and 8W treatments. These minute bark beetles do not compete with *Ips typographus* for food and space, and are probably not important prey for the predators and parasitoids in this study. The other 2 bark beetles *Pityogenes chalcographus* and *Dryocoetes autographus* and the cerambycid *Rhagium inquisitor* are potential competitors, but occurred in rather low numbers and probably they did not affect *Ips typographus* productivity much (*R. inquisitor* has a two-year life cycle and the larvae were still quite small when the bolts were peeled). Most of the predators and parasitoids found here can attack *P. chalcographus* and *D. autographus*. The abundance and relatively large size of most of the *Rh. tutele* and *R. xylophagorum* specimens that emerged suggest that they had fed on *Ips typographus*. Most *R. brevicornis* specimens were small (1–2 mm) suggesting that *P. chalcographus* was the main host. *Karpinskiella pityophtori* is considered to be a parasitoid of *Pityogenes* spp. (Hedqvist 1963).

Most of the predatory and saprophagous Coleoptera emerged as larvae in authumn. Forsslund (1941) reported that *Thanasimus* larvae overwintered mainly outside trees killed by *Ips typographus* in central and northern Sweden. Apparently this behaviour is common for several species, and it could be an adaption to the climate in the nordic region, where winters often are cold and larvae might not survive above the snow.

The sequence of arrival of the bark beetle enemies agrees with results of Stephen & Dahlsten (1976) from *Dendroctonus brevicomis* LeConte. In that study the arrival of the parasitic Hymenoptera, especially *R. xylophagorum*, was well synchronized with the development of the host; i.e. most arrived when the host was in the last larval instar or pupal stage. Other observations indicate that *R. xylophagorum* (Berisford et al. 1971) and *Rh. tutele* (Krüger & Mills 1990), the two dominant parasitoids in the present study, mainly attack those stages. *Tomicobia seitneri* attacks *Ips typographus* adults outside the tree. Thus the specimens of *T. seitneri* in the 0W treatment probably emerged from beetles that had been attacked before they were released in the cages.

The fact that *Ips typographus* and some of its natural enemies differed in their arrival and emergence patterns has practical implications. Forestry practices should be carried out in ways that minimize adverse impacts on bark beetle enemies. For example, bark beetle attacked timber should be removed from the forest before the peak arrival of the parasitoids, i.e. when bark beetle brood are in their late larval or pupal stages (around 1 July for *Ips typographus* in central Sweden). Present regulations in Sweden prescribe removal of *Ips typographus* attacked timber before 1 August, when bark beetle emergence usually starts. Furthermore, removal of colonized trees and timber after the autumn emergence of *Ips typographus* should be avoided. Most *Ips typographus* have emerged by 1 October, but predatory Diptera and parasitic Hymenoptera still remain and emerge the following spring.

The study demonstrates that bark beetle enemies in the nordic region, where most bark beetles have only one generation per year, can reach high enough densities to reduce bark beetle emegence to very low levels. The most important factors that influence the population density of these entomophages have yet to be identified. Forestry practices. e. g. clear-felling, thinning, removal of windthrown stems etc., strongly influence the distribution and abundance of bark beetles in time and space. However the numerical responses (reproductive and migratory) of bark beetle enemies to changes in prey density are poorly understood. Better knowledge in this topic may be essential to effectively integrate control of destructive bark beetles with management of forests.

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