

The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species

Jörg Müller · Heinz Bußler · Martin Goßner ·
Thomas Rettelbach · Peter Duelli

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Abstract The influence of natural disturbance on biodiversity is poorly known in the intensively cultivated landscape of Europe. As an example of insect disturbance we studied effects of gaps generated by outbreaks of the spruce bark beetle (*Ips typographus*) on biodiversity in the area of the National Park “Bavarian Forest” and compared them with openings (e.g. meadows) created by humans in these forests. Insects were sampled using flight interception traps across twelve ecotones between edges of closed forest, six bark beetle gaps and six meadows. The diversity and species density of true bugs and of bees/wasps increased significantly from the closed stand to the edge, and continued to increase inside the openings at interior and exterior edges. Species density in saproxylic beetles also increased significantly from closed forest to opening, but only across ecotones including bark beetle gaps. Similarly, the number of critically endangered saproxylic beetles increased significantly in bark beetle gaps. Using indicator species analysis a total of 60 species were identified as possessing a statistically significant value indicating preference for one of the habitat types along the ecotones: 29 of them preferred gaps, 24 preferred

J. Müller (✉)
National Park “Bavarian Forest”, Freyunger Str. 2, 94481 Grafenau, Germany
e-mail: joerg.mueller@npv-bw.bayern.de

H. Bußler
Bavarian State Institute for Forestry, Am Hochanger 11, 85354 Freising, Germany
e-mail: Heinz.Bussler@t-online.de

M. Goßner
Loricula – Agency for Canopy Research, Ecological Studies and Determination, Schussenstr. 12,
88273 Fronreute, Germany
e-mail: martin.gossner@loricula.de

T. Rettelbach
Fritzenanger 9, 83362 Surberg, Germany
e-mail: rettelbach@freenet.de

P. Duelli
Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürichstrasse 111,
8903 Birmensdorf, Switzerland
e-mail: peter.duelli@wsl.ch

meadows, three were characteristic for edges of meadows, three for edges of bark beetle gaps, but only one was typical of closed forest. Most of our results support the thesis that *I. typographus* fulfils the majority of criteria for a keystone species, particularly that of maintenance of biodiversity in forests. Our results emphasize the value for the study and conservation of insect diversity of the policy of non-interference with natural processes pursued in some protected areas. As a recommendation to forest management for increasing insect diversity even in commercial forest, we suggest that logging in recent gaps in medium aged mixed montane stands should aim at retention of a part of the dead wood. Planting should be avoided, to lengthen the important phase of sunlit conditions.

Keywords Bark beetles · Forest edge · Gaps · Saproxyllic beetles · True bugs · Bees and wasps · Insect outbreak

Introduction

After 5,000 years of civilisation history in Europe (Angelstam 1997; Grove 2002; Speight 1989), recorded experience on natural disturbance and its value for the maintenance of biodiversity is accordingly scarce. The majority of topics in conservation biology today deal with different conservation management practices in intensively used landscapes. However, the interest in natural, dynamic processes such as flooding (Dzioczek et al. 2006) or fire (Martikainen et al. 2006) and their influence on biodiversity is increasing. It is supposed that the understanding of natural dynamics is important for the development of suitable conservation management, even in an anthropogenic landscape. In forests, competition between humans and saproxyllic beetles has a long history (Grove 2002). The European spruce bark beetle *Ips typographus* is considered to be the most serious pest species of mature spruce stands, mainly of Norway spruce, *Picea abies*, throughout Eurasia (Grodzki et al. 2004; Wermelinger 2004). Among all types of forest damage from 1950 to 2000 in Europe, 2–9 million m³ per year of timber were destroyed by bark beetles, mainly *I. typographus* (Schelhaas et al. 2003). The preference of this species for mature spruce trees increases the economic impact of its damage. With regard to these facts it is not surprising that most published research on bark beetles deals with damage and prevention of outbreaks in commercial forests (Eriksson et al. 2006; Hedgren and Schroeder 2004; Reeve 1997; Wermelinger 2004). By contrast, some studies have pointed out the ecological value of *I. typographus* and other bark beetles as ecosystem engineers and so-called keystone species, driving forest regeneration, and producing snags and a rich patchiness in forest canopies (Jonášová and Pracha 2004; Martikainen et al. 1999). Apart from providing these ecosystem services, the arthropod complex associated with *I. typographus*, including more than 140 species (Weslien 1992), is in itself a significant contribution to diversity.

The ‘keystone species concept’, originally developed to describe the influence of a starfish’s predatory activities on “persistence and integrity” of a rocky intertidal community (Paine 1969), has been broadly applied over the years in ecology and conservation. Despite an ongoing debate about the validity of the concept, there is a growing consensus that a small subset of species can have a disproportionately large effect on ecosystems, compared to their abundance or biomass (Simberloff 1998). These keystone species are functionally linked to the persistence of an array of other species and play a critical role in the organization and/or functioning of the ecosystem. Mills et al. (1993) described five broad categories of keystone species, one of them being keystone habitat modifiers, also called ‘ecosystem engineers’ (Lawton and Jones 1995). The major changes in forest

structure, light regimes and increase in dead wood caused by *I. typographus* infestations in our study area are reasons for believing that this bark beetle plays the role of a keystone species in montane forests where spruce occurs in mixture or as the dominant tree species. The fact that *I. typographus* is alone amongst 35 bark beetle species in the study area in being able to kill larger numbers of mature Norway spruce trees indicates a low functional redundancy, integral to the concept of keystone species by Walker (1995).

The general importance for biodiversity of gaps in forests, especially windthrow gaps, is well known and demonstrated in numerous previous studies (Barbalat 1998; Fayt et al. 2006; Bouget and Duelli 2004). A general preference of many insects for forest edges exposed to the sun was revealed by studies at man-made forest edges adjacent to agricultural land (Duelli and Obrist 2003; Duelli et al. 2002a; Flückiger et al. 2002). Duelli (2006) even concluded that biodiversity of forests is concentrated mainly along their edges (Duelli 2006), and that what we usually call forest species are in fact mostly forest edge species (Wermelinger et al. 2007).

Before we can state that *I. typographus* is a keystone species, we have to show the high preference of other species for the habitat created by this bark beetle. To satisfy the criterion of low functional redundancy, this habitat should not be provided by other types of openings made by humans, such as meadows, which are also available in the montane zone.

Commercial forestry has in the past few centuries created dense and young forests throughout Europe. The current growing stock of European forests has a mean volume three times higher than in 1950 (Nilsson et al. 2001; Schelhaas et al. 2003), but large, old trees are rare (Hammond and Harding 1991; Speight 1989). There is also a lack of structural variation (patchiness) in our forests, caused by the rarity of gaps and interior edges. The immense alteration of natural processes involved in plantation forestry had a knock-on effect on the saproxylic fauna, with species becoming extinct or threatened by extinction (Müller et al. 2005a).

Natural openings in Central European forests are mostly gaps caused by windthrow or outbreaks of insect species such as bark beetles. In the National Park “Bavarian Forest” these kinds of events generally did not occur simultaneously in the past, but were nevertheless linked. Records of large scale windthrow events are available for approximately the last 130 years. However, a large bark beetle attack in the core zone, unaffected by management intervention for many years, offers the opportunity to study the influence of a natural disturbance process on biodiversity in a montane forest. This dramatic and rapid change to the forest induced a controversial discussion on policy throughout the region. The question “What are the ecological consequences of ‘wilding’ (that is, non-interference with natural processes) as a long-term conservation strategy?” was intensively discussed in the region, as also in many other European countries. The question was identified as one of the 100 most important ecological problems of high policy relevance in the UK (Sutherland et al. 2006). Hence, it is important to study natural processes which lead to changing habitat conditions in strictly protected forested areas, especially where such processes are controversial with respect to their effect on our carefully managed landscape.

Heavy bark beetle infestation creates openings in forest where non-interference may be practiced, as one management option. To assess the effects of this “opening-up” process on biodiversity and compare it to man-made openings, such as meadows, we studied assemblages of three species-rich insect groups, which include typical forest insects (saproxylic beetles, true bugs and wasps/bees) along ecotones from gaps/meadows, across interior/exterior edges into closed forest, in the montane-mixed forest zone. To assess the role of *I. typographus* as a keystone species in a forested montane landscape, this project addressed the following questions:

1. Does species density and diversity alter along a horizontal transect across bark beetle gaps, forest edges and closed forest?
2. Does the diversity pattern along ecotones from bark beetle gaps to closed forest differ from ecotones from meadows into the forest, therefore allowing a low functional redundancy for *I. typographus* to be stated?
3. Do habitat preferences of species for gaps, meadows, exterior and interior edges, and closed stands support the keystone hypothesis?
4. Is species density in tree crowns similar to that near ground level in open areas, and therefore a suitable alternative habitat for sun-loving species, even in dense forests?

Materials and methods

Study area

The study was carried out in the National Park “Bavarian Forest”, a 24,000 ha mountainous region in South-eastern Germany (Fig. 1). Average daily temperatures range from 3.5 to 6.5°C with an average annual precipitation of 1,100–1,500 mm. The mean duration of snow cover is about 5–6 months in the zone studied; the vegetation period is 184 days. In contrast to the majority of German landscapes, the forested area of the National Park was settled late by humans, in the 15/16th centuries (Strobl and Haug 1993). Up to now, settlements were restricted to small clearings in the forest landscape. In the first 300 years of settlement, glassworks were responsible for most harvesting of wood. Despite a partly intensive logging in their immediate surroundings, the natural tree species composition was little affected. Furthermore, at the end of this period in 1850 stands of virgin forest still existed, especially in the upper montane zones. Within several decades in the late 19th and early 20th century, modern forestry altered tree species composition by the planting of mainly spruce after shelterwood logging and on areas windthrown or killed by bark beetles. In 1970 the first

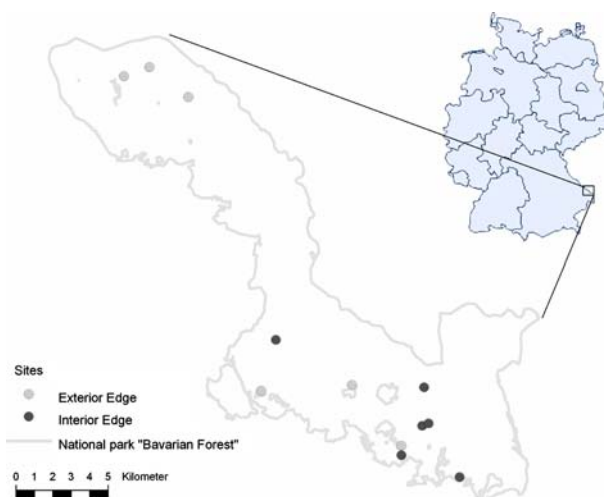
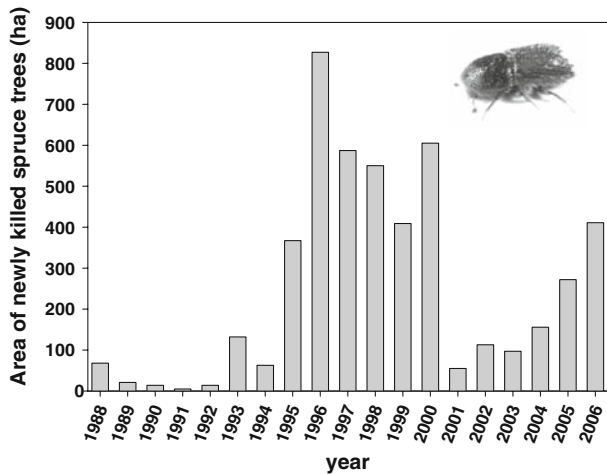


Fig. 1 Study area National Park “Bavarian Forest”. The distribution of the 12 investigated transects across forest edges are shown. For more details see Müller et al. (2007a)

Fig. 2 Yearly area of newly infested spruce trees in hectares, mainly by European bark beetle *Ips typographus*, in the area of the National Park “Bavarian Forest” (in total 20% of the area)



National Park in Germany was founded in this area, resulting in a phasing-out in the core area of the Park of all logging activities. Today, the lower montane zones are dominated by mixed stands of mainly spruce *Picea abies*, beech *Fagus sylvatica* and a low percentage of silver fir *Abies alba*, while in the upper montane zone (>1,162 m) stands of *P. abies* still dominate, as in the time before human interference. Disturbances in this montane forest are older than modern forestry, introduced in the late 19th century. Historical sources report on destruction of forest in 1786 by windthrow and in 1796 by bark beetle. In the 19th century eight windthrows are recorded caused by severe storms in 1868 and 1870, followed by an extensive bark beetle outbreak in the subsequent years, especially in the virgin forests at higher altitudes (Strobl and Haug 1993). This seems similar to the process at present underway (Fig. 2). In old literature, it is remarked that even in untouched virgin forest, gaps caused by windthrow and bark beetle infestation, with huge amounts of standing and lying dead trees are regularly found (Hennevogel 1905). This indicates that disturbance by storm and bark beetle occurs naturally and widely in this montane forest ecosystem (Elling et al. 1987). Induced by several storms in the 1980s and a succession of hot summers in the 1990s, a large outbreak of *I. typographus* started, first with large areas of infestation at higher elevations, later at lower altitudes through the whole mixed montane zone (Fig. 2). This process has operated entirely without interference, because of the policy of no pest management followed in the core zone of the National Park. From an ecological point of view, a highly diverse pattern of patchiness with glades was created, especially in the mixed montane zone, containing forest plants and huge amounts of dead wood. The boundaries between gaps and closed forest represent a widely spread system of interior edges. In contrast, as a result of settlement history within the NP, some exclaves comprising meadows and former pastures exist. Edges of these features are distinguished below as exterior edges. They are dominated by plants of meadows and pastures.

Sampling transects

We selected 12 widely separated sites (Fig. 1): six at interior and six at exterior forest edges (for details see Müller et al. 2007a). The year of infestation of the six bark beetle gaps studied varied from 1993 to 2003. Investigated gaps and man-made openings were similar in size (bark beetle gaps 1.1–13.8 ha, mean 6.8 ha; meadows 0.5–12.0 ha, mean 6.5 ha), and

altitude (gaps, mean 897 m; meadows, mean 908 m). Until now, bark beetle attack has been concentrated in the South-East of the NP. Therefore the sites with interior edges were located mostly in this part of the area. Because stand structures are similar throughout the whole of the NP, the three exterior edges in the North-West are directly comparable with the other studied edges. On each ecotone we installed five traps. The first was placed in the gap or on the meadow, 40–70 m distant from the last tree at the edge, 1.5 m above the ground; the second at the last shrub or tree on the edge, also 1.5 m above the ground; the third installed with aid of a crossbow in the crown of the last tree at the edge at a height of 15–25 m, depending on the tree height; the fourth placed similarly in a tree crown in the forest interior, 60–80 m distant from the edge; the fifth under this tree, 1.5 m above ground. The distance of the last trap from the edge seems to us to be sufficient, according to previous studies on edge effects (Grimbacher et al. 2006; Wermelinger et al. 2007). To avoid sampling bias caused by differences in insect species density on the different tree genera *Picea*, *Abies*, *Fagus* and *Acer* we selected an equal number of deciduous trees for sampling in the exterior and interior edge categories as well as in the closed forest. All transects were located in mixed stands of deciduous and coniferous tree species. We did not measure habitat variables such as the amount of dead wood or the availability of inflorescences, but in all cases the amount of dead wood was higher in the bark beetle gaps, and inflorescences were more abundant in the open areas than in surrounding closed forests. For testing preferences at the species level we used the following five habitat types: opening/gap, interior/exterior edge, closed forest. To assess vertically differentiated preferences, we compared samples from canopy traps with those of strata nearer ground level.

Sampling of insects

Insects were sampled during 2006 using flight interception traps as a standardised method. This is one of the most frequently used methods for sampling beetles and true bugs in comparative studies of forests under different types of management (Basset et al. 1997; Grimbacher et al. 2006; Grove 2000; Kaila et al. 1994; Martikainen et al. 2000) and has also proved suitable for sampling bees and wasps (Müller et al. 2005b). Similarly to other types of traps, such as pitfall or Malaise traps, flight interception traps measure insect activity, with more individuals sampled at sites with higher activity. However, the higher activity in the species of our study is clearly related to availability of better quality habitats for mating, egg laying or feeding (Bense 1995). Therefore, we followed this widely used approach (Hyvärinen et al. 2006; Similä et al. 2003), already successfully applied in edge studies (Grimbacher et al. 2006), to compare species density in different types of stands. Traps consisted of a crossed pair of transparent plastic shields (40 × 60 cm) with a funnel of smooth plastic material attached to the bottom and a plastic roof at the top. To attract species searching for flowers, a yellow, adhesive tape was applied to one of the shields. At the end of the funnel a 1 l sampling jar filled with killing and preserving agent (1.5% copper-vitriol-solution) was mounted. The traps operated during the whole growth period of 5 months and were emptied each month (May–September) by filtering the collecting fluid through a tea strainer and transferring the catch to 70% ethanol.

Species included in the study

We focused our study on three taxonomic groups of insects: (I) saproxylic beetles (Coleoptera), which are dependent, during some part of their life cycle, upon dead or dying wood of moribund or dead trees (standing and fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics (Schmidl and Bußler 2004; Speight 1989). Highly

endangered species were only represented in this group, according to the red data book for Bavaria (Schmidl et al. 2003). (II) True bugs (Heteroptera) are primarily plant-sap feeders and/or predators. (III) Bees and social wasps (part of the Hymenoptera Aculeata) are typical visitors at inflorescences.

All specimens of the investigated groups were determined to species level. Determination was done by the authors, who are specialists for their groups, using the following literature: Coleoptera, HB (Freude et al. 1964–1983), Heteroptera, MG (Péricart 1972, 1983, 1987, 1998), TR (Osten 2000; Schmid-Egger and Wolf 1992; Westrich 1989). Reference specimens are deposited in the Bavarian State Collection of Zoology (ZSM), Munich. The complete list of species determined was published in Müller et al. (2007a). Based on this data, we calculated as response variables the species density as represented by the number of species per trap (Gotelli and Colwell 2001) and the diversity using the Shannon-Index (Magurran 1988) per trap.

Statistical analysis

To analyse the data across the three categories of opening (gap/meadow), edge and forest on each transect, we used the single trap in the opening and the two traps each at the edge and in the forest. This is an unbalanced sample design. Due to this fact, the global hypothesis of independence between the three spatial zones across the forest edges (gap/meadow, forest edge, closed forest), and the comparison of the spatial zones of the two types of edges (transect across interior and exterior forest edge) and each of the response variables were assessed by means of resampling-based multiple testing (Westfall and Young 1993). This nonparametric procedure allows for inferences to be made without imposing distributional assumptions, like normality or homoscedasticity, on the data. The situation is typical for insect trap data. The *P*-values obtained by this procedure were adjusted for multiple comparisons utilizing a step-down max-*T* approach (Algorithm 2.8 in Westfall and Young 1993), which ensures high power of the test procedure while controlling its family-wise error rate. For each response variable (species density, diversity), a post-hoc test (Tukey all-pair comparisons) was additionally applied to assess the differences in the rank transformed response variables between each pair of categories (Hothorn et al. 2006). The statistical analysis is based on implementations of the above procedures in the add-on package “coin” (Hothorn and Hornik 2005) within the R system for statistical computing (version 2.4.1, R Development Core Team 2006). To detect and describe the value of different species for indicating environmental conditions in the spatial categories (horizontal: gap/meadow, interior edge/exterior edge, closed forest; vertical: near forest floor, canopy) we used the Indicator Species Analysis (Dufrière and Legendre 1997). This method produces an indicator value (IV) for each species by combining information on the concentration of species abundance in a particular category and the faithfulness of occurrence of a species in a particular category. It produces indicator values for each species in each category, which are tested for statistical significance using a Monte Carlo technique. Only species with a *P*-value <0.05 were accepted as indicator species. Species diversity was calculated using the Shannon Index. For both analyses PCORD 4.0 was used (McCune and Mefford 1999).

Results

Analysis was based on a total of 365 species: 204 saproxylic beetles (4,124 specimens), 96 true bugs (2,301 specimens) and 65 bees and social wasps (1,888 specimens).

Distribution of species density and diversity across horizontal transect

The species density of saproxylic beetles increased significantly across the interior edges, from closed forest to the opening (bark beetle gap). Across the exterior edges, species density did not differ between edge and opening (meadow), but in both it was significantly higher than in closed forest. For true bugs and bees/wasps (Fig. 3) the increase of species density across interior and exterior edges from closed forest to edge and openings was significant and similar in both types of edges, but the difference between edges and openings was not significant.

The Shannon Index applied to saproxylic beetles revealed no significant difference between the three types of zone across the horizontal transect (Fig. 3). Diversity of true bugs was higher in interior gaps than at their edges or in closed forest, and at exterior edge sites significantly higher in meadows than in closed forest. For bees/wasps the diversity was significantly higher at the edges and openings, for both types of forest edges, compared to the closed forest (Fig. 3).

The trends of an increase of species density and diversity were very similar across interior edges caused by bark beetle and exterior edges caused by humans (Fig. 3), with one exception. However, the increase of species density of saproxylic beetles from forest to opening was significant only for the bark beetle gaps, but not for the meadows. This is also true for the critically endangered saproxylic beetles. We found significantly higher numbers of specimens only in bark beetle gaps (Fig. 4).

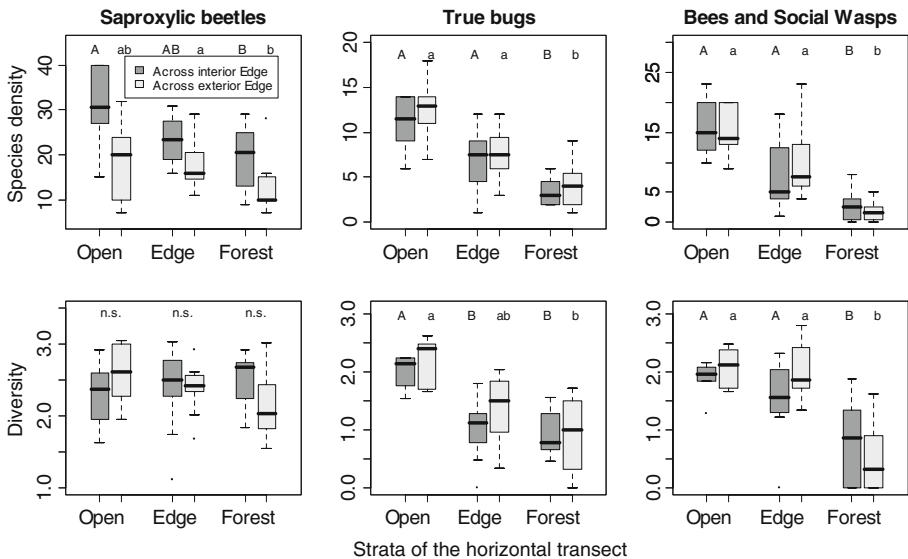
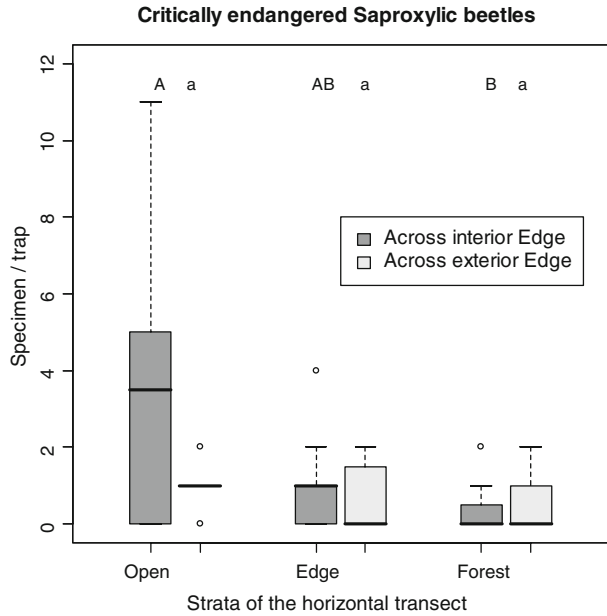


Fig. 3 Species density and diversity (median) of three groups of insects along a horizontal transect across interior forest edges (dark grey), open (gap), forest edge, and closed forest and across exterior edges (pale grey) with open (meadow), forest edge and closed forest. The two types of transects were tested separately (number of traps per transect type: open 6, edge 12, forest 12), as marked with lower- and upper-case characters. Different letters indicate significance of Tukey post-hoc tests, non significance is indicated by n.s.

Fig. 4 Specimens (median) of critically endangered species per trap (RL Bavaria 2003 (Schmidl et al. 2003). Categories: least concern, endangered, critically endangered) along the horizontal transect across forest edges. The three categories were tested separately across interior and exterior edges, as marked with lower and upper-cased characters. For a detailed species list see Müller et al. (2007a)



Habitat preference of species

Using indicator species analysis, 60 insect species showed a significant indicator value for one of the five horizontal habitat types (Table 1). Most of these species (29) preferred the bark beetle gaps in forests, followed by the meadows (24 characteristic species). Three species each preferred exterior or interior edges, but only one the closed forest. The number of characteristic species varied among the three taxonomic groups. For saproxylic beetles, gaps (11 species) seem to be most important, but several species were characteristic for meadows (7 species). Two species could be identified as characteristic for exterior edges and five for interior edges. Only one species was found to prefer closed forests. Among the true bugs, species with significant indicator values could only be found for gaps (4) and meadows (9). Within the bees and social wasps the number of indicator species was highest in forest gaps (12), followed by meadows (8), whereas only one species showed a preference for exterior edges, and none could be found for the other strata.

Comparing strata at tree crown and near forest floor levels (Table 1) we found 4 saproxylic beetles characteristic for the canopy, but 13 at ground level. Among the true bugs seven species, mostly specialised on a particular tree genus (Table 1), were typical for the canopy, and only one for the stratum near ground level. Within the bees and social wasps no species was found to be typical for the canopy, but seven species were characteristic for the lower stratum.

Discussion

Species depending on particular zones

Along the ecotones from opening to forest we found in all three taxonomic groups a high number of species with a preference for gaps and meadows. Even if accompanying

Table 1 Preference of single species for a zone/stratum of the horizontal and vertical transects, using indicator species analysis (IV = indicator value, $P = P$ -value) (Dufrêne and Legendre 1997)

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	P	Canopy	Forest ground	IV	P	Biology
Number of traps	6	12	6	12	24			24	36			
Coleoptera												
<i>Anthaxia quadripunctata</i>	3	2	1		38.6	0.007	1	5				Larva xyloph. in fresh CWD, adults on flowers
<i>Tritoma bipustulata</i>	10	2		1	35.6	0.018	1	12				Larva mycetophagouse on wood inhabiting fungi
<i>Gaurotes virginea</i>	4	3	5	3	30	0.036	2	13				Larva xylophagouse in advanc. Decompos. CWD, adults on flowers
<i>Curtimorda maculosa</i>	2		1		28.2	0.033		3				Larva xylo-mycetoph. in advanced decomposed CWD
<i>Mordella holomelaena</i>	3		2		25.7	0.041		5				Larva xylo-mycetoph. in advanced decomposed CWD
<i>Leperisinus fraxini</i>	2	2			24.6	0.044	3	3				Larva xyloph. in fresh CWD
<i>Scaphisoma agaricinum</i>	2		2		21.8	0.048		4				Larva mycetophagouse on wood inhabiting fungi
<i>Ischnomera caerulea</i>		6			25	0.04	5	1				Larva xylophagouse in advanced decomposed CWD
<i>Tillus elongatus</i>		13			25	0.038	11	2				Larva zoophagouse (Scolytidae) in advanced decomposed CWD
<i>Stenurella melanura</i>	9	4	181	5	92	0.001		201	51.4	0.001		Larva xylophagouse in advanc. Decompos. CWD, adults on flowers
<i>Pityogenes chalcographus</i>	13	74	398	164	76	0.004	87	638	66.7	0.022		Larva xyloph. in fresh CWD
<i>Judolia sexmaculata</i>			10	2	60.6	0.001		12				Larva xylophagouse in advanc. Decompos. CWD, adults on flowers

Table 1 continued

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	P	Canopy	Forest ground	IV	P	Biology
<i>Lepturobosca virens</i>			18			50	0.001		18			Larva xylophagouse in advanc. Decompos. CWD, adults on flowers
<i>Ampedus nigrinus</i>	1	17	155	309	12	48.1	0.027	311	183			Larva xylophagouse in advanced decomposed CWD
<i>Nudobius lentus</i>		1	6			46.2	0.002		7			Larva zoophagous in fresh CWD
<i>Pachytodes cerambyciformis</i>	1		10	3		39.4	0.017		14			Larva xylophagouse in advanc. Decompos. CWD, adults on flowers
<i>Crypturgus hispidulus</i>		1	5	3	4	31.2	0.034	5	8			Larva xyloph. in fresh CWD
<i>Anobium pertinax</i>		1	8		1	30.5	0.018		10			Larva xylophagouse in advanced decomposed CWD
<i>Crypturgus cinereus</i>		1	3	1	4	30	0.032	2	7			Larva xyloph. in fresh CWD
<i>Malthodes hexacanthus</i>			7	9	4	28	0.043	2	18			Larva zoophagouse in advanced decomposed CWD
<i>Dasytes niger</i>	1		7			28.5	0.02		8			Larva zoophagouse in advanced decomposed CWD
<i>Leptusa pulchella</i>			2	1		26.7	0.042		3			Larva zoophagouse in advanced decomposed CWD
<i>Dasytes obscurus</i>	1	3	32	39	1	58.8	0.002	28	48			Larva zoophagouse in advanced decomposed CWD
<i>Ampedus erythrogonus</i>	1	5	4	32	7	36.7	0.039	35	14			Larva xylophagouse in advanced decomposed CWD
<i>Aplocnemus tarsalis</i>		2		10		34.7	0.012	6	6			Larva zoophagouse in advanced decomposed CWD
<i>Hedobia imperialis</i>		2	1	2	31	42.1	0.009	18	18			Larva xylophagouse in advanced decomposed CWD
<i>Polygraphus poligraphus</i>	3	17	1	45	38	53.2	0.002	76	28			Larva xyloph. in fresh CWD

Table 1 continued

	Meadow				Closed forest	Forest ground				Biology
	Exterior edge	Gap	Interior edge	Canopy		IV	P	IV	P	
<i>Ermobius abietinus</i>	6		3	11	2		20.8	0.009	Larva xylophagous in advanced decomposed CWD	
<i>Anaspis thoracica</i>	1	1	26	28	2	2	19.9	0.043	Larva xylo-zoophagous in advanced decomposed CWD	
<i>Aplocnemus nigricornis</i>	1		5	6			16.7	0.026	Larva zoophagous in advanced decomposed CWD	
<i>Hylastes cunicularius</i>	1	15	7	6	58		54.4	0.002	Larva xyloph. in fresh CWD	
<i>Dasytes plumbeus</i>	26	39	14	11	4	4	45.4	0.01	Larva zoophagous in advanced decomposed CWD	
<i>Xyloterus lineatus</i>	1	5	6	5	34		39.8	0.014	Larva mycetoph. in fresh CWD	
<i>Platycerus caprea</i>	1	10	4	4	13		38.1	0.006	Larva xylophagous in advanc. Decompos. CWD	
<i>Cychramus variegatus</i>	1	3	6	1	11		35.5	0.007	Larva mycetoph. on woodinhabiting fungi	
<i>Dryocoetes autographus</i>		3	14	3	28		28.8	0.032	Larva xyloph. in fresh CWD	
<i>Xyloterus domesticus</i>	1	2	3	37	31		28.6	0.008	Larva mycetoph. in fresh CWD	
<i>Rhagium mordax</i>	5	10	4	2	8		28.4	0.034	Larva xyloph. in fresh CWD, adults on flowers	
<i>Hylecoetus dermestoides</i>	1	4	2	47	39		25.7	0.015	Larva xylo-mycetoph. in fresh CWD	
<i>Pteryngium crenatum</i>	1	1	6	1	4		23.7	0.03	Larva mycetophagous on wood inhabiting fungi	
<i>Bibloporus bicolor</i>	1	1	3	8	3		20	0.03	Larva zoophagous in advanced decomposed CWD	
Heteroptera										
<i>Orthops kalmii</i>	3		1		52.7	0.001	4		Herbivorous, mostly on Apiaceae	
<i>Megalonotus chiragra</i>	2				40	0.006	2		Mostly open area habitats, polyphagous, fruit-eating	

Table 1 continued

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	P	Canopy	Forest ground	IV	P	Biology
<i>Rhyparochromus pini</i>	2					40	0.008		2			Open area habitats, polyphagous, fruit-eating
<i>Plagiognathus arbustorum</i>	7	1				37.8	0.014		8			Succession sites, zoo-herbivorous
<i>Carpocoris purpureipennis</i>	10		3			32	0.02		13			Open area habitats, herbivorous herbaceous plants
<i>Leptopterna dolabrata</i>	2	2				28.2	0.029		4			Open area habitats, herbivorous Poaceae
<i>Saldula orthochila</i>	2		1			28.2	0.028		3			Shores, Zoophagous
<i>Tingis pilosa</i>	2	1	1			28.2	0.015		4			Open forests, herbivorous on Lamiaceae
<i>Lygus gemellatus</i>	2	1	1			24.6	0.044		4			Open area habitats, herbivorous Artemisia
<i>Palomena prasina</i>	1		29	5		73.9	0.001	3	32			Herbivorous, arboricolous
<i>Dolycoris baccarum</i>	30	2	56	33		51.1	0.007	4	117	40.8	0.003	Herbivorous, arboricolous
<i>Dictyla convergens</i>			7			33.3	0.016		7			Herbivorous on Myosotis
<i>Orius minutus</i>			2			30.8	0.027		2			Zoophagous, mostly on Aphidina
<i>Cremnocephalus alpestris</i>	12	266	2	474	263			981	36	77.2	0.001	Coniferous trees, zoo-herbivorous, feeds on Aphidinae
<i>Pentatoma rufipes</i>	2	96	5	52	29			154	30	69.8	0.001	Deciduous and coniferous trees, zoo-herbivorous
<i>Psallus varians</i>	4	94	12	205	126			367	74	62.2	0.022	Deciduous trees, zoo-herbivorous, Fagaceae
<i>Atractotomus magnicornis</i>	1	9	1	7	6			19	5	31.8	0.011	Coniferous trees, zoo-herbivorous, feeds on Aphidinae
<i>Phytocoris dimidiatus</i>		2		5	15			19	3	30.1	0.005	Deciduous and coniferous trees, zoo-herbivorous

Table 1 continued

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	P	Canopy	Forest ground	IV	P	Biology
<i>Acomporis alpinus</i>		3		2	1			6		16.7	0.03	Coniferous trees, zoophagous on Aphidinae
<i>Dicroscytus intermedius</i>		6		3				9		16.7	0.022	Coniferous trees, herbivorous
Aculeata												
<i>Bombus pascuorum</i>	52	18	42	23	7	49.3	0.007	10	132	56.6	0.001	Open areas, polylectic
<i>Andrena helvola</i>	9	11	1		2	48.5	0.004	1	22	26.8	0.021	Open areas, forest edges, Asteraceae, Grossulariaceae, Liliaceae, Rhamnaceae, Rosaceae
<i>Bombus lucorum</i>	99	43	108	25	6	45.3	0.042	34	247	54.7	0.021	Open areas, open forests, meadows, polylectic
<i>Dolichovespula norvegica</i>	5	8			2	34.3	0.022	6	9			Montaine forests, nest by wood
<i>Bombus hypnorum</i>	2			1		33.1	0.015	1	2			Open forests, forest edges, polylectic
<i>Vespula rufa</i>	6		2	2		28.2	0.036	2	8			Open areas
<i>Andrena haemorrhoa</i>	10	6	2		1	27.8	0.049	1	18			Open areas, forest edges, polylectic
<i>Dolichovespula sylvestris</i>	2				1	18.1	0.034		3			Forests, open area, nectar feeder
<i>Vespula vulgaris</i>	3	16	1	1	3	43.3	0.013	6	18			Open areas
<i>Apis mellifera</i>	44	9	386	71	26	79.5	0.004	39	497	69.2	0.003	Honey bee
<i>Hylaeus confusus</i>	3	4	33	14	5	58.7	0.002	14	45			Forests edges, succession sites, wood-inhabiting in beetle galleries and Rubus, polylectic
<i>Andrena lapponica</i>	5	25	74	60	16	58.5	0.003	63	117			Boreo-montane, oligolectic, specialised on Vaccinium
<i>Bombus bohemicus</i>	45	17	88	7	9	56.3	0.011	15	151	44.9	0.015	Cuckoo on <i>B. lucorum</i> , Taraxacum, Centaurea, polylectic

Table 1 continued

	Meadow	Exterior edge	Gap	Interior edge	Closed forest	IV	P	Canopy	Forest ground	IV	P	Biology
<i>Bombus sylvestris</i>	8	5	29	8	4	52.4	0.008	7	47	39.9	0.019	Cuckoo on <i>B. pratorum</i> , Taraxacum, Knautia, Centaurea
<i>Bombus pratorum</i>	7	9	30	13	17	46.6	0.013	24	52			Open forests, meadows, polylectic
<i>Bombus hortorum</i>	2		5			45	0.001		7			Forest edges and attached meadows, gardens, polylectic
<i>Lasioglossum ruftarise</i>		2	13	13		42.3	0.014	4	24			Montane species, forest edges, polylectic
<i>Lasioglossum subfulvicorne</i>	1	4	14	14	1	38.2	0.03	2	32	31.4	0.022	Forest gaps and edges, polylectic
<i>Bombus jonellus</i>	3	7	11	13		37.3	0.024	16	18			Open areas, mires, heath, polylectic
<i>Lasioglossum lativentre</i>	6	6	10	7		35.2	0.027	8	21			Forest edges, succession sites, polylectic
<i>Hylaeus annulatus</i>			2			33.3	0.017		2			Montane species, forests, wood-inhabiting
Sum of signif. species	24	3	29	3	1			12	22			

All specimens per habitat category are given, for species with $P < 0.05$ the P -values are given. The category is indicated by number of specimens in bold face. Species are arranged according to their preference for horizontal categories. The number of traps per category is also shown. CWD = coarse woody debris

environmental factors were not measured in present study, current studies (Müller, unpubl. data) in the same area prove that highest density of flowers occurs in gaps and meadows and the highest amount of dead wood in the bark beetle gaps. Moreover, the determinants for individual species can be validly discussed using existing knowledge. Most adults of the saproxylic beetles and Aculeata with a preference for openings are typical blossom visitors (Table 1). We explain the preference of other saproxylic species (e.g. *Ampedus auripes*, *Anobium pertinax*, *Leptusa pulchella*, *Malthodes hexacanthus*, *Nudobius lentus*) for gaps by a higher diversity and availability of dead wood structures. The volatiles emitted by recently dead and dying wood attract several species of Scolytidae, such as *Pityogenes chalcographus*, *Crypturgus cinereus*, *C. hispidulus* (Bußler and Müller 2004; Rohde et al. 1996). Of the blossom visitors without a connection to dead wood, the bees *Andrena haemorrhoa*, *A. helvola*, *Bombus hypnorum*, *B. lucorum*, *B. pascuorum* and the wasps *Dolichovespula norvegica*, *D. sylvestris*, *Vespula rufa* showed a preference for meadows, whilst the bees *Andrena lapponica*, *Apis mellifera*, *Bombus bohemicus*, *B. hortorum*, *B. jonellus*, *B. pratorum*, *B. sylvestris*, *Lasioglossum lativentre*, *L. rufitarse*, *L. subfulvicorne* preferred gaps. This agrees with other studies of Aculeata in forest openings (Flückinger 1999; Kuhlmann 2000).

Among the true bugs those species with a preference for meadows (Table 1) are typical inhabitants of open habitats. They feed on plants characteristic of ruderal and successional areas. Species with a preference for gaps are more typically associated with woodland or forest, as are the at least partly arboricolous *Dolycoris baccarum* and *Palomena prasina*. Previously published results report open areas and edges in forests to be preferred to closed stands by many other groups of arthropods, e.g. ground beetles (Carabidae) (Bedford and Usher 1994; Grove and Yaxley 2005), sawflies (Symphyta) (Flückinger 1999), flies (Diptera) (Bächli et al. 2006), hoverflies (Syrphidae) (Fayt et al. 2006), neuropterans (Neuroptera) (Duelli et al. 2002a) and spiders (Araneae) (Flückinger 1999).

There are several explanations for why the number of species with a preference for closed forest was low in the present study: firstly, our studied taxa are all insects, whose activity is more or less positively related to temperature, which is higher in openings than closed forest. Studies on insects restricted to closed canopies, or the interior of forests, are lacking in Central Europe. Additionally, most forest-dwelling insects are more strongly influenced by structural features such as dead wood colonized by fungi (Jonsell et al. 1999; Ódor et al. 2006), than by canopy cover, where these have not been attacked by bark beetles, the mature, formerly commercially managed stands of our study area possess a poor variety of lower vegetation, fungi and dead wood structures. However, we have to keep in mind that in old-growth beech forests a high diversity of dead wood structures can also be found in closed stands (Christensen et al. 2005), together with a rich saproxylic fauna (Müller et al. 2007b). Among taxa other than the insect groups studied here, such as birds, bryophytes or lichens, several species are well known to be strongly associated with closed stands (Nilsson et al. 1995; Saetersdal et al. 2004). A further reason for the absence in the present study of species characteristic of closed forest is the history of settlement in Europe, involving an extensive alteration of forest in all areas by clearance or intensive logging. Thus, those species strictly associated with large, unlogged forest landscapes must be expected to have become extinct centuries ago in all but a very few regions (Müller et al. 2005a; Speight 1989). Studies in forested areas with large old-growth stands do in fact report even on beetle species characteristic of the forest interior (Grove and Yaxley 2005).

Gaps versus meadows

For all taxa, our results showed higher species density only in bark beetle gaps. Additionally, we found species with significant value as indicators for either gaps or meadows. In general, open habitats in forests are patches in a shifting mosaic, whose inhabitants are open habitat generalists, forest edge or glade specialists, but also multi-habitat species which need both tree-covered and open habitats in order to complete their life cycle (Fayt et al. 2006). As already discussed, such gaps caused by windthrow or the collapse of overmature trees were present even before modern forestry started to alter the forests of the study area. These sites provide warmer microclimates, which are especially preferred where temperature is a factor limiting the survival of populations (Warren and Key 1991), as in the montane zone of the National Park “Bavarian Forest”. Meadows adjacent to forests have a richness and diversity of Aculeata and Heteroptera similar to that of gaps. This can be explained by the inflorescences and a high diversity of plant species, which are provided by both types of openings but not by closed forests. Moreover, differences in leaf chemistry and architecture of shrubs and tree saplings compared to mature trees may play a role for sap-sucking insects (aphids, true bugs) (Schowalter 1985). This is also supported by the increase of Aculeata species during the first several years on a spruce windthrow gap in an alpine forest (Duelli et al. 2002b; Wermelinger et al. 1995). Our species indicator analysis found different species characteristic for meadows and gaps in all three taxonomic groups. In meadows a greater number of ubiquitous species was found (Table 1), especially among the true bugs. In gaps most of the recorded species were inhabitants of complex habitats and occurred only where inflorescences, trees and dead wood are available together. Even if richness patterns of gaps and meadows are similar, a higher species density of saproxylic beetles, including the threatened species, was found only in gaps. Therefore we can conclude that the quantitative species density in meadows and gaps is dissimilar, and that the latter support a larger number of species characteristic for forest conditions and specialists requiring complex forest habitats. This underscores the importance of *Ips typographus* as a habitat engineer within forests.

Canopy as alternative habitat to edges/openings

The number of species found in the tree crowns was relatively low. This agrees with studies on several taxonomic groups in Central European forests (Bächli et al. 2006; Hacker and Müller 2007; Wermelinger et al. 2007). In contrast, species of some groups such as jewel beetles, several true bugs and the lace wings are often more abundant in the canopy (Floren and Schmidl 1999; Gruppe et al. 2007; Gruppe and Müller 2006; Schubert and Gruppe 1999; Wermelinger et al. 2007), but with the exception of true bugs these were poorly represented in our study (Müller et al. 2007a). Trees with green branches down to ground level, a normal condition for edge trees, offer an opportunity to trap or collect even typical arboricolous canopy species such as true bugs and some saproxylic beetles close to the forest floor (Gruppe et al. 2007; Stork et al. 2001). The apparently low number of species with a preference for the canopy in our study was influenced by this descent of normally canopy-dwelling species at the edges. It must be concluded, however, that in temperate forests the availability of dead wood, young trees and herbaceous species near the ground results in general in a more diverse habitat for insects than that provided by tree crowns.

Ips typographus as a keystone species

The definition of keystone species is primarily based on the observation that in many ecosystems certain species have an unusually high number of relationships with other organisms in their community (Simberloff 1998). The definition has been expanded (Menge et al. 1994), so that species may also qualify as keystones by virtue of how they change the environment, e.g. beavers *Castor canadensis* because of their dams (Naiman et al. 1986), gopher tortoises through their burrows which form a home for other species (Jackson and Milstrey 1989) or European bee-eater *Merops apiaster* which provides food and places to nest and roost for many other species in arid areas (Casas-Crivillé and Valera 2005). Christianou and Ebenmann (2005) defined three types of keystone species based on theoretical models of extinction. Using this classification *I. typographus* can be identified as the abundant intermediate species type, interacting strongly with many resources. A high keystone index (Jordán et al. 2006) can also be attributed to *I. typographus* not only because of the high number of species directly interacting with it (Weslien 1992), but also as shown by our study because of the numerous other forest insects which benefit from bark beetle gaps. However, this definition of keystone species can be further restricted by the consideration of low redundancy as a criterion (Kotliar 2000). If this bark beetle could be excluded, windthrow would produce similar openings in the study area, as shown to have existed in past centuries even under old-growth conditions and in the 1980s also in former commercial stands. A direct comparison between windthrow areas and beetle gaps was not possible in this study, because recent windthrow gaps were not available. But we have to keep in mind that bark beetles produce a structure which nevertheless shows some clear differences to windthrow gaps; with more snags than lying trees, and no root plates. The reality in Central European montane forest is that windthrow and *I. typographus* occurrence are strongly linked in forests containing spruce, and can probably only theoretically be separated in the landscape. However, we can conclude that within the area of the National Park, by driving a process resulting in greater diversity of insect taxa in formerly commercial, dense forests, the former pest species undoubtedly fulfils the majority of criteria for a keystone species.

Management implications

The keystone concept is a useful tool for communicating the importance of ecology to the public (DeMaynadier and Hunter 1994), especially in species with bad public reputations, such as the most feared bark beetle species in Central European forestry. The study of uncontrolled disturbance regimes teaches us much about insect “calamities” in montane forests. It is important to stress that in the montane zone most insects seem not to be edge species as indicated by Duelli (2006), but gap species as shown in our study. Coming back to the question of the ecological justification for “wilding” (non-interference with natural processes), we conclude that insect disturbance on the landscape scale is an important factor in the maintenance of biodiversity. It results in more complex habitat conditions, which benefit other insects. In the area of the National Park “Bavarian Forest” the infestation by bark beetle has created sunny openings and caused an increase in dead wood availability. In relict old-growth stands with a relict saproxylic fauna, an attack also increases availability of dead wood (Müller et al. 2005a). This is a first step on the way back to an increased structural diversity of the forest landscape and could save from extinction some of the saproxylic species which still survive as “living dead” in isolated refuges (Müller et al. 2007a).

Whilst not denying these important ecosystem services, we have to observe that Norway spruce plantations are widely distributed today even at lower altitudes, where conditions are much more favourable for *I. typographus* than in montane forests. As a consequence of this, but exacerbated by climate warming, we have to expect a further increase of spruce tree infestation by bark beetles in the near future (Jönsson et al. 2007). This is not likely to be viewed positively by the forest industry, because of serious economic penalties. From an ecological point of view, a large scale infestation where spruce is the only tree species could negatively influence other forest species (Koprowski et al. 2005; Scherzinger 2007). On the other hand, studies on soil fauna in the montane spruce forest have shown that logging of infested spruce stands at high elevations results in the extinction of rare Collembola, while release of bark beetle areas by non-interference sustained this soil fauna (Rusek, pers. commun.). In conclusion, we derive from our study the following recommendations for conservation in montane, forested areas of Central Europe:

1. Bark beetle infestations in montane forests have been typical for this habitat even before modern forestry began, and many insect species benefit greatly from the increase of habitat diversity and temperature found in bark beetle gaps.
2. For economic reasons, uncontrolled infestations will be restricted to protected areas. However, the creation wherever possible of similar gaps, even in logged forests, would benefit forest-dwelling insects in general.
3. To simulate this type of natural disturbance, logging in medium-aged mixed montane stands should aim to create gaps with retention of a part of the dead wood. Planting after logging should be delayed, to lengthen this important phase of sunlit conditions otherwise rarely found in a landscape of young and dense commercial forests.

Finally, the application of the keystone species concept to *I. typographus* improves our understanding of the effects of natural disturbance on biodiversity, beyond the prevailing, purely economic views on this serious pest.

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